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Theoretical Derivation of Numerical Thinning Schedules for Douglas-Fir

BY
GEORGE R. STAEBLER

NEXT TO THE AX AND GOOD JUDGMENT, yield tables are probably the forester's most important management tool. Normal yield tables prepared for many commercially important tree species show volumes of stands, usually based on site and stand age, which have been judged empirically to be fully stocked. Empirical yield tables show yields to be expected in non-normal stands, based on average stocking found on a given property or in a given region. Important information on growth and stand development may be derived from both kinds of tables. Fundamentally, however, they are most useful for determining the expected yields from unmanaged stands harvested at the end of the rotation, with no intermediate cuts.

Logically, the next step is the development of yield tables for managed stands—stands in which intermediate harvests (thinnings) are made before the final cut. Such tables are commonly thought of as experience tables, which show yields resulting from a given method of management. As such, they require a vast amount of information gathered over many years—probably decades. The urgent need for yield tables for managed stands makes it imperative that some method be devised for producing them long before the required experience figures become available.

Published gross yield tables for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Staebler 1955b) may serve as a first approximation of managed-stand yield tables for this species. These tables show the total volume of wood produced on specified sites at various ages. The total volume includes the standing live volume (from normal yield tables) and the volume of trees that died before any given age.

Recovery of full gross yield would require a plan of management providing for salvage of all normal mortality. The central feature of such intensive management is likely to be a progressive thinning program designed to mold the stand to some desired end, in addition to recovering all mortality. Inevitably, the forester will be required to formulate the necessary thinning schedules.

A scheme is proposed here for making schedules for Douglas-fir, using the gross yield tables for the species. The method is theoretical in that it has never been tried and is based on a number of assumptions. The logic of the scheme is appealing, however, and the mathematical systematization of the problem provides a concept upon which a thinning regime may be built.

Method

We may assume that the gross yield in cubic volume of a normal, unmanaged stand represents the maximum production of which the site is capable and cannot be increased by cultural or management prac-

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tices. The periodic gross increment for any age period in the life of a normal stand likewise represents the full capacity of the site to produce wood in a stand of the chosen age. Further, we may assume that approximately full increment may be produced with widely different combinations of growing stock, tree size, and radial increment. The mathematical relation between these factors has been determined for a forest "model" in which all trees are the same size and growing at the same rate (Staebler 1958). Assuming such a model, the forester may specify how fast he wants trees to grow, and—knowing how much wood an acre can produce—he may determine how many trees growing at the chosen rate are required to fully utilize the capacity of the site. Calculation of the number for successive age periods produces a thinning schedule—a guide to the orderly reduction in number of trees as stand age increases (Staebler 1955a).

This derivation of a thinning schedule is a reversal of the method used to construct experience yield tables for managed stands. Such tables are based on experiments involving different methods of thinning or management, the effects of which are appraised by comparing resulting yield and tree size. Increment and tree size are dependent variables. In the scheme just proposed, we assume we know this increment —the full capacity of the site measured in volume of wood produced—and we specify the size of tree we want to produce. Then we calculate the thinning schedule required to achieve the predetermined result.

Increment must be measured in cubic volume of the entire stem since this is the only commonly employed unit of measure that has biological significance.

More complete justification of the underlying assumptions and stand development theory will be found in later sections of this article, after the method is described in its entirety.

Calculation of the thinning schedule is best explained by an example. Table 1 shows the steps required to work out a schedule for site II (site index 170) Douglas-fir. Column by column, the explanation is as follows:

Column 1. "Age in years" is the age at which the stand is to be thinned. Hence a decision regarding the interval between thinnings must be made to set up this column. In this instance the chosen interval is the number of years most closely corresponding to a 10-foot increase in total height of dominant and codominant trees as determined from site curves (McArdle *et al.* 1949).

Column 2. "D.b.h." Attained diameter obtainable or desirable is the heart of the proposed scheme. The forester, keeping in mind the limitations of the species, decides the size trees he wants to grow and the growth path by which they shall reach the desired size. The thinning regime is designed specifically to achieve this objective. Thus, if rapid diameter growth and large size at young ages are wanted, few trees widely spaced will be required. If slow growth (narrow rings) is desired, many trees closely spaced will be retained. In the example, the chosen diameter growth is considered somewhere near the practical maximum attainable for the species. It is assumed that trees will average 8 inches d.b.h. at 20 years. Desired diameter growth in the 21st year is 0.5 inch, decreasing 0.0035 inch with each passing year so that in the 121st year growth is 0.15 inch. Diameter at the given ages is calculated from this growth rate.[1]

Column 3. "Total height" is taken from the site index curve for s.i. 170 (McArdle *et al.* 1949), which shows the average height of dominants and codominants at the chosen ages.

Column 4. "Volume per tree" in cubic feet, total stem, is taken from standard volume tables (McArdle *et al.* 1949), interpolating for d.b.h. and total height from

[1]Attained d.b.h. =
$$-2.735 + 0.57175\,(\text{age}) - 0.00175\,(\text{age})^2$$

TABLE 1. Computation of a thinning schedule calculated to produce 41-inch Douglas-fir trees on site II at 120 years.[1]

Age in years (1)	D.b.h. (2)	Total height (3)	Volume per tree (4)	Periodic growth per tree (5)	Gross yield (6)	Periodic gross increment (7)	Stems required (8)	Stems before thinning (9)	Stems removed (10)	Volume before thinning (11)	Volume removed (12)	Volume after thinning (13)	Total yield (14)	Cubic ft. normality after thinning (15)
	Inches	*Feet*	*Cu. ft.*	*Cu. ft.*	*Cu. ft.*	*Cu. ft.*	*Number*	*Number*	*Number*	*Cu. ft.*	*Cu. ft.*	*Cu. ft.*	*Cu. ft.*	*Percent*
20	8.0	44	7.29		1,550			212.6	27.3	1,550	199	1,351	1,550	87
				4.55		843	185.3							
23	9.5	54	11.84		2,393			185.3	39.1	2,194	463	1,731	2,393	75
				5.84		854	146.2							
26	10.9	64	17.68		3,247			146.2	25.3	2,585	447	2,138	3,247	69
				7.14		863	120.9							
29	12.4	75	24.82		4,110			120.9	19.6	3,001	486	2,515	4,110	65
				11.44		1,159	101.3							
33	14.2	85	36.26		5,269			101.3	14.6	3,673	529	3,144	5,268	65
				13.43		1,164	86.7							
37	16.0	95	49.69		6,433			86.7	10.0	4,308	497	3,811	6,432	65
				15.18		1,164	76.7							
41	17.8	104	64.87		7,597			76.7	8.5	4,976	551	4,425	7,597	65
				25.44		1,736	68.2							
47	20.3	114	90.31		9,333			68.2	7.3	6,159	659	5,500	9,331	67
				32.65		1,990	60.9							
54	23.0	124	122.96		11,323			60.9	5.2	7,488	639	6,849	11,319	71
				39.60		2,206	55.7							
62	26.0	134	162.56		13,529			55.7	3.6	9,055	585	8,470	13,525	75
				40.47		2,107	52.1							
70	28.7	144	203.03		15,636			52.1	2.7	10,578	548	10,030	15,633	79
				49.93		2,466	49.4							
80	31.8	154	252.96		18,102			49.4	2.0	12,496	506	11,990	18,099	84
				52.18		2,471	47.4							
91	34.8	164	305.14		20,573			47.4	1.6	14,464	488	13,976	20,573	89
				68.11		3,120	45.8							
107	38.4	174	373.25		23,693			45.8	0.5	17,095	187	16,908	23,692	97
				47.40		2,145	45.3							
120	40.7	181	420.65		25,838			45.3	..	19,055	..	..	25,839	..

[1]Data are for 1 acre, where appropriate.

Columns 2 and 3. The volumes were carefully curved, using age as the independent variable to eliminate vagaries due to irregularities in the base table.[2]

Column 5. "Periodic growth per tree" is the growth in cubic feet between the ages given in Column 1 and is obtained by subtracting successive values of attained tree volumes in Column 4.

Column 6. "Gross yield," taken from the gross yield table, represents the total production of the site up to the given age.[3] It is presumed to represent the maximum production of which the site is capable, and cannot be increased by management.

Column 7. "Periodic gross increment" is the gross increment between the ages

[2]Log volume =
$-6.61449 + 7.92738$ (log age)
-1.67570 (log age)^2

[3]The gross yield tables give yields only at 10-year intervals. Since the thinning schedule requires yields at in-between ages, the tables were curved to permit determination of volume for these ages without having to resort to straight line interpolation. The following equation was obtained by integrating a third degree equation fitted to the 10-year increments read from the gross yield tables between ages 20 and 120 years, and adjusted to pass through the point where age equals 20 and gross yield equals 1,550:

Gross yield =
$3{,}574 + 225.69$ (age)
$+1.9385$ (age)$^2 - 0.021866$ (age)^3
$+0.00005883$ (age)^4

given in Column 1 and is obtained by subtracting successive values in Column 6. As a corollary to the gross yield assumption just stated, periodic gross increment represents full productive capacity during the period in question.

Column 8. "Stems required" is the number of trees per acre, growing at the desired rate (Col. 5), required to absorb the full productive capacity of the site (Col. 7) in the corresponding age period. It is calculated by dividing Column 7 by Column 5. Thus the gross yield table shows (under the assumptions stated) that an acre of site II land supporting a 20-year-old stand will produce 843 cubic feet of stem wood between ages 20 and 23. If each tree on that acre grows 4.55 cubic feet in the interval, 185.3 stems per acre are required to fully utilize the site. Between 23 and 26 years, only 146.2 stems are required since each grows 5.84 cubic feet, and the acre can produce 854 cubic feet.

Column 9. "Stems before thinning" at any age is the number of trees that were retained (or required) in the previous period. Thus the figures duplicate those in Column 8 except that at age 20, 212.6 trees are shown as present in the stand. This figure is derived by assuming that the stand contained the normal volume, 1,550 cubic feet, shown by the normal yield table. It is further assumed that silvicultural treatment before age 20 was such that the trees are well spaced and average 8 inches d.b.h., or 7.29 cubic feet. Thus, 212.6 trees (1,550 ÷ 7.29) would be present on the acre.

Column 10. "Stems removed" is the difference between the number of stems present before thinning and the number required for the ensuing period, or Column 9 minus Column 8.

Column 11. "Volume before thinning" is the product of number of trees before thinning and the volume per tree, or Column 9 multiplied by Column 4.

Column 12. "Volume removed" is the number of trees removed times their average volume, or Column 10 multiplied by Column 4. (All trees are the same size in the forest "model" assumed.)

Column 13. "Volume after thinning" is the volume before thinning less the volume removed (Col. 11 minus Col. 12).

Column 14. "Total yield" is the volume of the stand before thinning plus the accumulated volume of thinnings to date. It is the same as Column 6, except for errors due to rounding, and serves as a check on calculations in the intervening columns.

Column 15. "Normality after thinning" is the ratio between the volume left after thinning and the normal volume for the age and site given in normal yield tables.

To summarize: Columns 1 and 8 make up the desired thinning schedule. Column 1 shows the ages at which the stand is to be thinned. Column 8 shows the number of trees to be left after each thinning. This is the maximum number of trees growing at a chosen rate that an acre of site II land can support, assuming the land is producing all the wood of which it is capable. In theory, retaining more than the indicated number of trees will reduce diameter growth since the wood produced must then be distributed over more trees. Retaining fewer trees would result in greater diameter growth.

Columns 11 through 14 make up the volume part of a managed-stand yield table. The difference between the standing volume (Col. 11) and the total yield (Col. 14) is the cumulative volume of the thinnings to date. Although the volume of growing stock is much different from that in the normal forest (Col. 15), the yield of the managed forest is exactly the same as the gross yield of the normal forest.

Justification

This method of determining thinning schedules is a purely mensurational approach, and only as good as the biological assumptions that underlie it. We need to

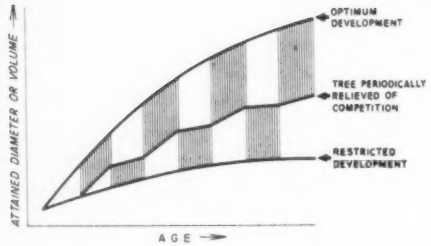

FIGURE 1. *Schematic diagram of individual tree development (assumed), showing how trees periodically relieved of competition will grow alternately at the optimum rate and at the restricted rate.*

inquire into the validity of these assumptions.

The steps that rest on biological assumptions mostly concern (1) thinning interval and intensity of cut, (2) diameter growth rate, (3) gross increment and possibilities of growth redistribution, and (4) the forest "model" assumed.

Interval and intensity of thinning. Interval of thinning is important for its effect on tree development. We might visualize optimum tree development, in terms of volume or diameter, as following a steeply ascending curve as trees grow older (Fig. 1). Competition between trees restricts development, causing the tree to follow a much lower curve. Periodic relief from competition permits trees to develop at somewhere near the optimum rate until competition is restored, after which development tends to parallel the curve of restricted development.

It is desirable to time thinnings so that a high proportion of the tree's development curve parallels the curve of optimum development. Intensity (magnitude of relief from competition) and frequency of thinning are obviously complementary factors in achieving this objective. Overly heavy thinnings will forestall competition for a long period and lengthen the interval between thinnings. Yield, however, will be reduced because the trees will not occupy the site completely for some time after thinning. It therefore seems preferable to choose an interval and intensity compatible with the tree's capacity to absorb new room.

The speed with which trees can absorb new growing space depends on the rate of crown development, which in turn is largely a function of age. Young trees grow rapidly in both height and diameter; crowns, and probably root systems, expand quickly. Removal of a single tree leaves a relatively small hole. On the other hand, crowns of old trees expand much more slowly and one tree occupies a relatively large space. Hence, thinnings should be made frequently in young stands and the interval gradually lengthened with age. Thinning coincidentally with some fixed increase in total height effectively relates frequency of thinning to the trees' capacity to absorb new room. The 10-foot height interval chosen for the thinning schedule presented in Table 1 is prescribed for coniferous plantations in England (Forestry Commission, 1951). Wilson (1951) has prescribed thinning with each 7- or 8-foot increase in height for red pine (*Pinus resinosa* Ait.).

The intensity of the cut, or the new room afforded remaining trees at each thinning, is automatically adjusted to the chosen interval by the diameter growth desired and the gross increment expected in the period between thinnings. To the extent that estimates of interval, gross increment, and diameter growth are based on sound biological principles, so also should the volume removed at each thinning be soundly based.

Diameter growth. We need next, then, to examine the biological assumptions behind the preconceived diameter growth rate. The question becomes, for example, "Will the 86.7 stems per acre (Table 1) left after thinning at age 33, which have a history of development such as is afforded by prior stand treatment, really grow at the rate of 0.45 inch per year during the next 4 years?" Prior stand treatment has re-

sulted in a tree with a certain diameter and a unique crown and root system—resulting largely from the growing space it has enjoyed to date. Presumably, trees 33 years old on site II and 14.2 inches in diameter must have a certain volume of live crown —no more, no less—if they are to grow 0.45 inch in diameter annually. It is precisely at this point that corroborative evidence is lacking. Will the trees have properly developed crowns to grow at the specified rate?

Certainly, the desired growth cannot be greater than that of open-grown trees growing at or near the maximum for the species. At the other extreme, diameter growth must be greater than that characteristic of dense stands. In a dense stand, diameter growth varies widely from tree to tree. Some trees are efficient growers, others inefficient. Also, suppression mortality should be expected. Under such conditions average diameter and diameter growth are not suitable for determining the number of trees to be retained after a thinning. Calculations based on the forest model, where all trees are the same diameter and grow at the same rate, would not apply.

Definitive data are not available to determine whether the growth rates chosen for Table 1 are realistic. Data from permanent sample plots in a well-stocked 78-year-old site II stand on the Gifford Pinchot National Forest make the growth rates up to 80 years appear capable of attainment. In this stand the largest 49.4 trees per acre (the number retained between ages 70 and 80 in Table 1) averaged 24.5 inches compared to 31.8 inches called for in the schedule. The 100 remaining trees (which would not be present had the stand been thinned by the proposed schedule) averaged 15.7 inches in diameter.

One would have to be a pessimist, indeed, if he believed that the diameters calculated for age 80 in the thinning schedule could not have been achieved in the Gifford Pinchot stand by repeated careful thinnings begun prior to age 20.

The diameter assumed at age 20 (8 inches, Table 1) appears easily attainable on the basis of limited plantation experience. Two site II plots covering 1.0 acre in a 21-year-old lightly thinned plantation on the Olympic National Forest showed that the largest 185 trees in the stand following the first thinning averaged 7.8 inches in diameter, ranging from 7 to 11 inches. In the next 5 years, these 185 trees grew an average of 0.3 inch per year—well below the planned 0.5 inch in the thinning schedule. However, this growth was attained in the presence of 647 competitors 2 inches and larger in diameter. In fact, 110 trees died because of competition in the 5-year period. If the total basal area growth of the stand had all been added to the 185 stems, the resulting growth per tree would have averaged 0.5 inch annually.

Diameter growth used in the schedule decreases as the trees get older, in line with the observation that trees growing under natural conditions are seldom able to maintain constant growth for any extended period (Baker 1950, p. 332; Spurr 1952, pp. 213-214; Duff and Nolan 1953; Hawley and Smith 1954, pp. 362-363). A specific diameter growth, however, is assumed to be an objective of management, and a thinning schedule is set up to achieve the objective. The objective might equally well be constant diameter growth over the rotation. The declining rate is used here simply because it is believed more realistic and more likely to be obtainable.

Gross increment and growth redistribution. Assumption that gross increment in unmanaged stands represents full growth capacity of the site is the third biologically based factor requiring critical examination. Closely related is the assumption that this growth may take place on widely varying amounts of growing stock. Justification for the first assumption comes largely from experiments designed to study the second.

Review of evidence, mostly European, concerning relation of growth to growing stock led Hawley and Smith (1954, p. 354) to make the following broad and tentative generalization: "The total pro-

duction of cubic volume by a stand of given composition on a given site, is for all practical purposes, constant and optimum for a wide range of density of stocking. It can be decreased, but not increased, by altering the amount of growing stock to levels outside this range." It is pointed out that growth includes the total production of wood in the boles of all trees, including those that die of suppression.[4] Heiberg (Möller *et al.* 1954, introduct.) in his discussion of Möller's work points out that Möller's theory — essentially that given above—has been tested extensively only for beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) in Europe, and remains to be tested for other species in other climates in other countries.

Small-scale, long-time American thinning studies in eastern white pine (*Pinus strobus* L.) plantations do seem to fit this pattern, however, in that total production of thinned and unthinned stands is nearly equal (Spurr *et al.* 1957; Wahlenberg 1955). In the Biltmore plantations described by Wahlenberg, reserved growing stock in the thinned stand averaged about two-thirds that in the unthinned stand.

No data collected specifically to test Hawley and Smith's generalization are available for Douglas-fir. It has been commonly observed, however, that unmanaged stands, whether overstocked or understocked, tend to approach normal by yield table standards (Meyer 1933; Briegleb 1942; Briegleb and Girard, 1943). That is, net growth in overstocked stands is less than normal, and in understocked stands greater than normal. It is possible that the explanation will be found in differences in mortality; more volume dies in overstocked stands and less in understocked, whereas gross increment is the same in both instances (Staebler 1955b).

However, analysis of board-foot growth on permanent sample plots in Douglas-fir (Johnson 1955) showed that net growth in stands covering a range of stocking (but still essentially well-stocked) tended always to be normal, and the stands remained understocked or overstocked by a constant volume. Trend toward normal, percentage-wise, was simply due to calculating the percentages from increasingly larger volumes. If both overstocked and understocked stands make normal *net* growth, it is unlikely that both also are growing at the normal *gross* rate. To do so would require that mortality be the same in overstocked and understocked stands, which is hardly plausible. It is possible, however, that board-foot growth, calculated only for the sawtimber trees in a stand and including only the merchantable portion of the stem, does not reflect cubic-foot increment characteristics.

The work of Briegleb (1942), although confirming in general a trend toward normality, showed that age is an important factor. Young stands with both below- and above-normal stocking (within certain limits) make supernormal growth. Stands older than 70 years, even those with below-normal stocking, make subnormal growth.

Briegleb interpreted his results to mean that the normal yield tables were low for young ages and high for older ages. Possible confirmation for young ages is found in British yield tables (Hummel and Christie 1953, Barnes 1955), which show a greater volume production for thinned Douglas-fir plantations up to age 50 years than the gross yield tables show for natural American stands. Differences between the British and American tables, however, may be due to the thinning practiced in the British stands, as well as to errors in the American tables.

This also makes suspect the generalization that increment is independent of management practiced. It is possible that thinning of the British stands *did increase* cur-

[4]It is probable that full production should be measured in total dry-matter production in stems, branches, roots, bark, and leaves. Stem volume is used because it is the only information available. Conceivably, stem volume increment may not be a constant proportion of total dry-matter production over a wide range of stand density.

rent annual growth. Hiley (1956, p. 107) points out that evidence on this point is conflicting, but concludes that on the average the amount of growing stock reserved does not materially affect increment. A study of high-yielding Danish, Prussian, and American stands of Douglas-fir, both thinned and unthinned, showed no evidence that thinning increased total gross increment (Briegleb 1952).

We may conclude that our estimate of gross increment in natural, untended stands of Douglas-fir is low for young ages and possibly high for older ages. True gross increment, if we knew it, should be a reasonable, possibly conservative, estimate of maximum production for the site. Furthermore, under management this production may be achieved over a considerable range of growing stock levels, though future research may well show an optimum level.

These possibilities of error do not seriously invalidate the method of constructing thinning schedules from present estimates of gross increment. We need only recognize that thinning schedules so constructed are without doubt subject to error, at least partly because of inadequate information on full productive capacity. Information on gross increment is frequently available to foresters from local plot data. Such data may be used to calculate schedules when they appear to more nearly fit conditions encountered.

The forest model. A thinning schedule could hardly be derived mathematically without extreme simplification through use of a model of some sort. For the schedule presented, essential features of the forest model are: All trees are the same size, and all trees grow at the same rate. This differs so widely from conditions found in natural, untended stands that the simplification is at first difficult to accept. Although variation in growth (and hence in attained diameter) of treees in untended stands is controlled partly by genetic makeup of the trees, environment (largely competition between trees, but also including microsite differences) is undoubtedly a much more important factor.

In a stand thinned regularly, on the other hand, competition is held to a minimum and, as far as possible, equalized between all trees. It is to be expected, then, that variation in growth between trees will be much reduced. That which does occur will result from genetic differences between trees and from differences in microsite.

Equalizing competition between trees infers creating a uniform spacing between trees. Obviously, spacing will not be uniform after every thinning. A spacing of 15 by 15 feet cannot be achieved by thinning a stand spaced precisely 14 by 14 feet. Hence, equal growing space for all trees cannot be maintained by repeated thinnings. Inevitable variations in growing space, coupled with normal genetic and microsite variations, will result in growth rates—and hence, diameters—varying over at least a restricted range.

Errors resulting from assuming complete uniformity in size and growth would be mostly reflected in volume of growing stock retained after thinning. Unless differences in size are entirely compensated for by diameter growth, trees larger or smaller than the size assumed are likely to be less efficient growers than the calculations show, and more growing stock will be required for the same increment per unit area. Also, if a range in sizes is present, trees cut in thinning are unlikely to have the same average diameter as those reserved.

It is impossible to say how closely the assumed model will fit conditions found in a continuously thinned stand. It seems plausible, however, that resulting errors will not be great.

Comparison with Other Schedules

In Table 2, other numerical thinning schedules that have been proposed for Douglas-fir are compared with the schedule developed from gross yield data. Age, diameter, and number of trees in the first three columns of the table are taken from Table 1.

TABLE 2. Comparison of published numerical thinning schedules with a proposed gross-yield schedule for Douglas-fir.

PNW Experiment Station				British yield tables			Hiley		Heiberg		
		Trees per acre									
Age in years (1)	Average diameter (2)	Gross yield (3)	Briegleb (4)	Age in years (5)	Average diameter (6)	Trees per acre (7)	Average diameter (8)	Trees per acre (9)	Age in years (10)	Average diameter (11)	Trees per acre (12)
	Inches	*Number*	*Number*		*Inches*	*Number*	*Inches*	*Number*		*Inches*	*Number*
20	8.0	185	235	19	7.4	430	7.5	420	28	5.7	629
23	9.5	146	202	22	8.5	335	9.0	260	31	6.4	532
26	10.9	121	178	25	9.8	280	10.5	185	34	7.2	436
29	12.4	101	158	28	11.0	240	11.9	150	38	8.2	339
33	14.2	87	130	31	12.2	210	13.3	110	42	9.5	267
37	16.0	77	111	35	13.3	180	15.1	85	46	10.6	213
41	17.8	68	95	40	14.6	156	17.3	65	50	12.0	171
47	20.3	61	76	45	16.0	138	19.5	45	55	13.7	136
54	23.0	56	--	50	17.3	125	--	--	60	15.3	108
62	26.0	52	--	--	--	--	--	--	66	17.3	85
70	28.7	49	--	--	--	--	--	--	72	19.4	68
80	31.8	47	--	--	--	--	--	--	78	21.5	56
91	34.8	46	--	--	--	--	--	--	85	23.6	47

From a study of high-producing, managed stands in Denmark and in the Pacific Northwest, Briegleb (1952) developed an equation showing the relation of the desirable number of stems to average height and diameter of the stand. Reserving the desirable number of stems following thinning is expected to insure near maximum growth of the stand. The equation is: Number of trees as percentage of normal for average d.b.h. $= -34.62 + 1.245 \times$ stand height as percentage of normal height for average d.b.h. Normal number of trees and normal height are from Bruce's revised yield table for Douglas-fir (McArdle *et al.* 1949).

Solution for the diameters and heights used for calculating the gross-yield schedule up to 47 years is given in Column 4 of Table 2. If the trees grow in diameter as planned in the gross-yield schedule, reserving the greater number called for by Briegleb's equation will result in correspondingly greater areal increment. For example, 235 trees growing 4.55 cubic feet each will result in a per-acre growth of 1,069 cubic feet in the 3-year period from 20 to 23 years, a figure 27 percent greater than the expected gross increment. In 47 years Briegleb's schedule would produce 46 percent more volume than gross yield. Apparently, either our estimate of gross increment—maximum production—is low, or the desirable number of trees calculated from Briegleb's equation could not grow as fast in diameter as called for in the gross-yield schedule.

Yield tables for conifers in Great Britain (Hummel and Christie 1953, Barnes 1955) are true managed-stand yield tables constructed from permanent sample plot data. Column 5 shows ages at which thinning is recommended, and Column 7 shows the recommended number of trees to be left for British site quality I. Site index is apparently between 150 and 160 feet, compared to 170 feet for the gross-yield thinning schedule. The 100 largest trees per acre produced by the schedule average 17.8 inches at 50 years, and all trees average 17.3 inches compared to 21.5 inches expected from the gross-yield schedule. Although the trees do not grow as fast in diameter as planned for in the gross-yield schedule, the greater number of trees per acre more than makes up for it, and yield at 50 years is nearly 50 percent greater

than the gross yield from the American tables for comparable site.

Hiley and Lehtpere (1955) proposed a method for constructing schedules for any desired thinning grade from the British yield tables referred to. The thinning grade is defined by the number of rings per inch grown on the 100 largest trees. As in the gross-yield schedule, the basic assumption is that increment per unit area is unaffected by thinning grade. For a constant increment per acre, thickness of the annual ring is inversely proportional to bole area, and may be altered by manipulating the bole area. The number of trees to be left after thinning is calculated from the required bole area. Use of Hiley and Lehtpere's method to calculate the number of trees required to make the 100 largest grow to the sizes planned in the gross-yield schedule gives the results shown in Column 9. Yield would be the same as that given by the British yield tables, but the far fewer trees would be larger.

Heiberg and Haddock (1955) proposed a thinning schedule for Douglas-fir on site index 150 beginning at 28 years (Cols. 10, 11, and 12). Their schedule is expected to produce trees with 6 rings per inch, with areal increment, based on Danish yield, considerably higher than given in the gross yield tables.

In general, these schedules call for many more trees at young ages than does the gross-yield schedule, but with more rapid reduction in numbers with succeeding thinnings. In all cases, yield—whether based on experience (British tables) or derived—is substantially larger than the gross yield on which the proposed thinning schedule is based.

Summary and Conclusions

"The complexities and simple magnitude of physical and biologic laws that affect man are so vast that no individual can grasp them all nor reduce their application in forestry to a mathematical basis alone. Art must always play a large role in man's husbandry of his essential resources." (Shirley 1955). The truth of this forester's tenet is unquestioned, yet every attempt to express biological laws mathematically leads unquestionably to better understanding and frequently opens to the forester new possibilities for the practice of his art.

Derivation of the gross-yield thinning schedule is such an attempt. The schedule is a rigorous, mathematical model based on quite easily defensible biological theory. It is presented as a logical method of regulating intermediate cuttings for production of full gross increment in trees growing at a chosen rate with a minimum of growing stock.

Thinning schedules are derived from gross yield tables for untended stands, assuming that (1) gross cubic-foot increment represents full poductive capacity of the site, and (2) this increment may be distributed over many or few trees. The forester, knowing how much wood an acre can produce, may determine how many trees growing at a specified rate are required to utilize the site's full growing capacity. Calculation of the number for successive age periods produces a thinning schedule.

To illustrate the method, a schedule has been derived for site II Douglas-fir, starting with 8-inch trees at age 20 and producing 40.7-inch trees at age 120. Far fewer trees per acre are required than are normally considered necessary for full stocking.

The derived schedule is compared to other proposed numerical thinning schedules for Douglas-fir. In general, these other schedules call for a greater number of trees, especially at young ages. It follows that if the trees attain the same size at a given age as in the gross-yield schedule, the greater-number-of-trees schedules must also yield more. This increased yield is not ruled out as impossible; the gross yield tables may underestimate production possible under intensive management.

In appraising possibilities of success of thinning schedules, it must be kept in mind that the aim is to produce trees of a certain size at a given age. Therefore, at any

given time proper stocking is more than a certain number of trees of a given size per unit area — the usual stocking criterion. We must have the proper number of trees of a given size *capable of growing at the prescribed rate*. Growth capability may be considered an added stocking dimension, depending on tree vigor, crown size, and supporting root systems. Number of trees per acre controls spacing; spacing controls crown size and root development; and crown size and root development control diameter growth. Hence, a neat balance must exist between spacing, roots and crown, and diameter growth, and this balance must be preserved if a numerical schedule is to succeed as expected. Starting with a per-acre growth potential, even granting that we know it imperfectly, seems to be a most logical way of maintaining the necessary balance as the stand develops.

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Mineral Nutrition of Trees

Mineral Nutrition of Trees (A Symposium). Duke University School of Forestry Bulletin 15, May, 1959. Durham, N. C. 184 pages. $2.50.

Review by Laurence C. Walker
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This volume records the 18 papers presented at a conference on the inorganic nutrition of forest trees held at Duke University in 1958. Subjects range from the highly specialized, such as the biochemical role of iron in plant metabolism, to status reports of research in forest tree nutrition by government, the forest industry, and academicians.

One of the most outstanding contributions is the chapter by Robert L. Barnes outlining a technique for the study of mineral requirements using excised tree roots. Basically, the idea is to compare the growth of minute root sections in a medium supplied with controlled quantities of nutrients, sugar, and vitamins. Thus plant material employed is genotypically identical, growing conditions are uniform, and confounding of results by microbial activity is prevented.

Many of the papers are excellent literature reviews. Thus, the eminent botanist Paul Kramer discusses the physiology of nutrition and Edward Hacskaylo summarizes the role of mycorrhizal fungi in enabling efficient utilization of available nutrients. A chapter on nutrient source materials for tree nutrition studies is especially helpful for forest researchers. Another paper outlines a technique for determining nutritional requirements of forest trees using automatic irrigation with extended day length. Thereby, many species can be kept growing continuously, obtaining the equivalent of two or more seasons growth in one year and providing for better estimates of growth response.

The section of the symposium entitled "The Diagnosis of Nutrient Status" concerns cultivated fruit trees. Inclusion of material on pines, spruces, and birch, about which considerable is known and in which foresters are more interested, would have been helpful. Likewise, foliar analyses and symptoms for evaluating nutritional deficiencies, it seems, would have been more appropriate if cited for white pine or scotch pine, rather than for orchard-grown tung.

Other noteworthy chapters discuss the determination of macro-element requirements of forest trees, statistical aspects of field studies, and horticultural and agronomic viewpoints on field experiments in tree nutrition.

There is much discussion of nitrogen, as there should be, in this book.

The foreword states that "recognition of the limitations in our knowledge of this subject provided both the stimulus for sponsoring this conference and a guide for planning its scope." In return, the Duke conference has been instrumental in lessening the limitations of knowledge and in providing a stimulus for experimental effort in the nutrition of forest trees. Forest researchers will long be indebted to those whose foresight arranged this symposium.

A Physiological Consideration of the Springwood Summerwood Transition in Red Pine

BY
PHILIP R. LARSON

THE TRANSITION from the formation of springwood to summerwood in trees of the temperate regions has presented an intriguing problem to foresters and physiologists alike for many years. Numerous researchers have recorded their observations of this phenomenon and some have advanced theoretical explanations of the process, but relatively few actual experiments have been established to scientifically test the proposed theories.

Among the theories that have been in vogue at various times in the past, the nutritional (Hartig, 1889) and the bark-pressure (De Vries, 1875) theories have probably evoked the most widespread discussions. Proponents of the nutritional theory felt that summerwood was dependent upon a change in metabolism due to the photosynthetic contribution of the newly formed and maturing leaves. Adherents to the bark-pressure theory proposed that summerwood resulted from the pressure of the newly formed xylem layers on the cambium. It was suggested that the tangential expansion of the bark could not keep pace with the rapidly expanding xylem; thus, the cambium was compressed by the cells lying to either side with the resultant formation of summerwood. Both theories were modified from time to time by various workers to fit existing conditions and observations. This early work has been extensively reviewed and criticized by Grossenbacher (1915).

Attempts have also been made to correlate the beginning of summerwood formation with various climatic factors. Midsummer drought has often been selected as a causative influence and it has, in some instances, shown a remarkable correlation. It is obvious, however, that drought, like many other factors, is but a secondary cause in that it exerts its influence on the overall growth of the tree or possibly on some structural part of the tree that is more intimately correlated with summerwood development. Midsummer droughts do not occur during every year or in every locale in the temperate regions, yet summerwood is formed almost without exception. Therefore, the correlative factor, to be effective, must be such that it will cause summerwood to form every year in spite of the local variations in climate and habits of growth.

Such a factor may be found in the pattern of growth exhibited by the vegetative buds and shoots of the tree. Experimental evidence accumulated over the years has shown quite conclusively that the initiation of cambial activity is correlated with the activity of the developing buds. An auxin or auxin-precursor emanating from these buds activates the dormant cambium in a

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basipetal direction along the branches and main stem. Much of this recent work has been reviewed by Wareing (1951), Larson (1956), and Stewart (1957).

Observational evidence suggests that during this period of active growth of the shoot, cells of the springwood type will be laid down, and the transition to the production of summerwood cells begins with the cessation of terminal growth and the setting of a new bud (Coster, 1928; Chalk, 1930; Priestley and Scott, 1936) or the maturation of the leaves (Wareing and Roberts, 1956). It has been further postulated that springwood may be correlated with a high auxin production during the period of rapid growth, and summerwood with a low auxin production when apical growth declines (Oppenheimer, 1945; Megli, 1955). The dependence of springwood formation on a relatively high auxin content has been tentatively demonstrated by production of "springwood-like" cells following exogenous applications of growth hormones (Söding, 1936; Brown and Cormack, 1937; Gouwentak, 1941; Fraser, 1949 and 1952).

The only recent work known to the author in which a serious attempt has been made to study the springwood-summerwood transition in conifers is that of van Buijtenen (1958). His objective was to study the influence of environmental factors on terminal growth and the types of wood formed in both seedlings and mature trees of loblolly pine (*Pinus taeda* L.). He found that in seedlings, an increase in temperature caused a reduction in tracheid wall thickness without influencing diameter whereas an increase in soil moisture resulted in an increase in tracheid diameter without influencing wall thickness. Long photoperiods had no consistent effect on either tracheid diameter or wall thickness. Irrigation and continuous illumination failed to elicit any response in either shoot growth or wood formation in mature trees. He concluded that a change in the condition of the tree itself, rather than some environmental factor, was responsible for the cessation of height growth and the initiation of summerwood.

The present study was based on the hypothesis that summerwood formation may be correlated with the cessation of terminal elongation and the setting of new buds through an auxin-mediated system.[1] To test this hypothesis, the study was designed with a twofold objective: (1) to determine the relationship between the cessation of terminal elongation and the transition of springwood to summerwood, (2) to determine the effect on growth-ring formation of exogenous applications of a growth hormone to decapitated seedlings.

Procedure

Red pine (*Pinus resinosa* Ait.) seedlings (2-2 stock) were potted in the spring of 1957 and maintained under nursery conditions until early October. At this time they were transferred to outdoor coldframes where they received the necessary cold exposure required to break dormancy. On December 16 the seedlings were brought into a greenhouse maintained on a schedule of about 72° F day and 62° F night temperatures. Day-length was artificially extended to 18 hours with warm-white fluorescent light supplemented with incandescent light.

The beginning of bud activity and extension growth was very uniform, and practically all seedlings were elongating by January 8. All lateral buds were pinched off as they developed in order to maintain growth control through the single apical bud. The study was divided into two experiments which will be described separately for convenience of presentation.

Experiment 1. It has been demonstrated by numerous workers that terminal growth can be prolonged in pines by long photoperiods whereas summer dormancy can be induced by short photoperiods (Wareing, 1956). If the hypothesis that summer-

[1]This is essentially the same hypothesis set forth by Wareing (1958) in an excellent review of the physiology of cambial activity.

wood development sets in following the cessation of elongation growth is valid, then summerwood should be produced in trees whose growth is arrested by short photoperiods. On the other hand, if a high auxin level is a prerequisite to springwood formation, then exogenous growth hormone applications may perpetuate springwood development in trees on short photoperiods.

The objective of this experiment was to arrest terminal growth by a short photoperiod and to attempt to perpetuate springwood formation in the same trees by artificial treatments. The treatments are shown in Table 1.

All seedlings were grown under long-day conditions until active extension growth was well under way. At this time (February 12) they were placed under the appropriate pretreatment daylength conditions. For short-day treatments, seedlings were placed in a ventilated, light-tight cabinet constructed over a greenhouse bench. The cabinet was opened at 8 am and closed at 4 pm daily.

After 3 weeks, measurable height growth could no longer be detected on the short-day seedlings although those on long days continued to elongate. At this stage (March 5) seedlings in treatments C to H were decapitated and the appropriate tip applications made. Indole-3-acetic acid (IAA) was selected for the exogenous tip applications. Approximately 1/10 gram of melted lanolin was dropped into 6 mm diameter cups made of aluminum foil. IAA was made up to a standard concentration and applied to the lanolin with a microburette in quantities of 10, 50, and 100 micrograms (μg) IAA per cup for treatments C, D, and E respectively. The cups containing the IAA-lanolin mixture were heated slightly over a water bath to assure even distribution of the IAA. Immediately following decapitation, the cups were inverted over the stem tips. The 1-percent gibberellic acid (GA)-lanolin mixture was applied in a similar manner.

Eighteen of the 24 seedlings in each treatment, C to H, were treated in the aforementioned fashion and the remaining 6 were treated by a cut-needle technique. The IAA was dissolved in a minimal quantity of 95-percent ethyl alcohol in small glass vials and made up to 2 ml solution volume with distilled water; the control, treatment H, was distilled water. Immediately following decapitation, the ends of 10 to 12 apical needles were severed and immersed in the solution. The vials were sealed with cotton and covered to exclude light. Uptake was completed within 1 to 2 days in all seedlings.

Collections, consisting of 3 seedlings from each treatment, were made at 4- to 7-day intervals over a 5-week period. Five stem segments were collected from each seedling as follows:

Sampling position in stem[2]	*No. annual rings*
(*a*) 1 cm below bud or decapitated tip	1
(*b*) 1 cm above base of current shoot	1
(*c*) Middle first internode	2
(*d*) Middle second internode	3
(*e*) 1 cm from soil line	4

The stem segments were fixed in formalin-acetic acid-alcohol (FAA). Unembedded sections (three for each stem segment) were cut on a sliding microtome, stained with safranin, and permanently mounted in Canada balsam.

Experiment 2. In its objective this experiment was similar to Experiment 1, except that in the first experiment an attempt was made to maintain springwood production and in Experiment 2 an attempt was made to produce false rings. If the premise of the proposed hypothesis is correct, summerwood should be produced when terminal growth ceases under short days and springwood produced when terminal growth is resumed under long days, resulting in a

[2]Hereafter the stem sections from the various sampling positions will be referred to by the letter assigned in this tabulation.

false ring. Substitution of growth hormones for the terminal bud should also produce a false ring, whereas debudded seedlings should continue producing summerwood until cambial dormancy sets in, regardless of daylength. The treatments are shown in Table 1.

Seedlings were grown on an 18-hour daylength until active height growth ceased and the new buds had begun to set; in contrast, in Experiment 1, growth was artificially arrested. At this time (March 21) they were placed under the appropriate pretreatment daylength conditions. Treatments began on April 11. Debudding consisted of merely removing the apical bud by a sharp bending movement. Decapitation, on the other hand, consisted of severing the stem tip approximately 0.5 to1.0 cm below the bud. Collections were made at weekly intervals over a 4-week period. Treatments Q and R were continued on long days throughout the summer and collected on October 29. All procedures pertaining to treatment and collection were identical to those of Experiment 1. In both experiments, daylength was considered merely as a research tool and no attempt was made to duplicate a photoperiodic control of growth in nature.

Results

Experiment 1. The cambia of all short-day seedlings in treatments B to H were still fairly active at the time of the first two collections and no summerwood cells[3] had been produced. Beginning with the third collection, relative differences could be detected in the production of summerwood-like cells.

In the apical sections, *a*, from decapitated seedlings the peripheral cells stained a deeper red. These cells formed a complete band around the periphery and were neither associated with reaction wood prevalent in many seedlings, nor absent in seedlings lacking reaction wood. The darker stained walls could first be observed in the new cells being laid down in collection 2, and by collection 3 a thin band of 1 to 2 dark-stained cells was readily discernible. Using this criterion, the number and size of the mature cells laid down following decapitation could be determined as shown in Table 2. Since the phenomenon did not occur in any of the undecapitated seedlings, average values for the five outermost cells

[3]Throughout this paper the term "cells" refers to secondary xylem tracheids and the term "cell wall thickness" refers to the thickness of the secondary cell wall.

TABLE 1. Pretreatment and treatments for experiments 1 and 2.

Experiment		Pretreatment,		No. seedlings in experiment—	
1	2	3 weeks	Treatment	1	2
A	I	Long-day	Long-day (control)	24	12
B	J	Short-day	Short-day (control)	24	12
..	K	Short-day	Long-day	..	12
C	L	Short-day	Short-day + 10 μg IAA on decapitated tip	24	12
D	M	Short-day	Short-day + 50 μg IAA on decapitated tip	24	12
E	N	Short-day	Short-day + 100 μg IAA on decapitated tip	24	12
H	..	Short-day	Short-day + lanolin on decapitated tip (control)	24	..
GA	GA	Short-day	Short-day + 1% GA on decapitated tip	6	12
..	Q	Long-day	Long-day throughout summer	..	12
..	R	Short-day	Long-day throughout summer	..	12
..	S	Long-day	Debud, long-day	..	12
..	T	Long-day	Debud, short-day	..	12
..	U	Short-day	Debud, long-day		12

TABLE 2. Mean number and radial diameter of cells produced in stem section a following decapitation and treatment.

Treatment[1]	Collection number[2] and days after treatment									
	4 (19)		7 (19)		5 (23)		6 (30)		8 (35)	
	No.	Dia.	No.	Dia.	No.	Dia.	No.	Dia.	No.	Dia.
		Microns		*Microns*		*Microns*		*Microns*		*Microns*
A-LD[3]	5.0	15.2	5.0	14.7	5.0	15.8	5.0	15.4	5.0	15.0
B-SD[3]	5.0	13.2	5.0	13.2	5.0	12.2	5.0	12.7	5.0	11.6
C-SD, 10 μg IAA	3.0	10.6	3.0	9.6	4.3	10.0	6.0	9.4	5.3	9.9
D-SD, 50 μg IAA	2.3	11.5	3.0	13.2	4.3	10.4	5.7	9.6	6.0	9.8
E-SD, 100 μg IAA	3.3	11.9	3.7	12.4	4.3	11.3	6.0	10.7	7.0	11.6
H-SD, lanolin	2.7	10.0	2.7	9.8	4.3	10.0	5.7	8.8	6.3	9.3

[1]LD = long day; SD = short day.
[2]Collections 4, 5, and 6 treated with lanolin; collections 7 and 8 by the cut-needle technique.
[3]Control treatments A and B, mean values for 5 outermost mature cells (see text).

for treatments A and B are given for comparison.

The bands of dark-stained cells were primarily restricted to the apical section, *a*, collected 1 cm below the point of decapitation. Although it was impossible to determine the number of cells produced by the cambia following decapitation in section *b*, measurements of the five outermost cells revealed the same pattern of variation; the differences, however, were smaller and the data are not given here. Cell measurements on the older sections, *c* to *e*, were erratic and inconclusive.

Obvious changes in cell wall thickness occurred in many treated seedlings during the course of the experiments. Numerous cell wall observations are included in the description of results.

The variation in radial diameter of cells in Table 2 can be interpreted on the basis of observable differences among treatments. Long-day treatment A promoted the continued production of large diameter, springwood cells. In the last two collections, 6 and 8, a few of the seedlings showed a slight thickening of the cell walls but there was no decrease in cell diameter.

A marked contrast was revealed by comparison of the short-day treatments B and H, which differed only in the fact that in the latter the seedlings were decapitated. Although summerwood production began at about the same time in both treatments, the development of the cells comprising the summerwood differed radically. In B, summerwood cells developed by a gradual thickening of the cell walls accompanied by only a slight decrease in radial diameter. In contrast, summerwood cells in H developed by a rather abrupt decrease in radial diameter following decapitation, with no increase in wall thickness.

Seedlings treated with 100 μg IAA (E) exhibited a somewhat different developmental pattern. In most seedlings, the cells decreased gradually in both diameter and wall thickness while in some seedlings three to four large-diameter cells followed decapitation and treatment. This pattern may be contrasted with the rather abrupt decrease in radial diameter of the cells in the untreated short-day seedlings (H). Fifty μg IAA (D) elicited a smaller response than 100 μg IAA in terms of cell diameter, whereas 10 μg IAA (C) and 1-percent gibberellic acid produced no observable treatment effects.

No consistent differences could be detected between the lanolin and the cut-needle-methods of treatment.

Experiment 2. The objective of this experiment, to produce false rings, was successfully accomplished by several treatments. The response to treatment, where

effective, was visually evident and quantitative data were therefore not recorded.

As in the previous experiment, 100 μg IAA, treatment N, elicited the greatest response from tip applications to decapitated seedlings. The production of thick-walled cells of the summerwood type was in progress at the start of this experiment and the effect of the short-day pretreatments was more pronounced than in Experiment 1. Several rows of narrow-diameter cells were present in sections of collection 1. By collection 2, large-diameter cells had begun to form in response to the IAA treatment and a definite false ring could be detected. The effect of IAA treatment was of short duration, however, and produced only 2 to 4 springwood-type cells (Fig. 1). Narrow-diameter cell production was again progressing by collection 4.

The response to 50 μg IAA, treatment M, was similar but less pronounced than in N. In collection 4, one seedling produced a conspicuous false ring while in 2 seedlings the false ring consisted of several rows of cells with only slightly larger diameters than the adjacent summerwood-type cells. There was no evidence to indicate that IAA, as applied in this study, induced the formation of compression wood tracheids as reported by Wershing and Bailey (1942), Fraser (1952), and Wardrop (1957).

The remaining tip applications, 10 μg IAA (L) and 1-percent GA showed no effect of treatment; a continuous band of summerwood cells was produced.

In terms of false-ring production, seedlings transferred to long days following the short-day pretreatment responded 100 percent. The formation of false rings could be readily traced through the successive collections in K. In collection 2, the new cells to the outside of the pretreatment summerwood band were large in diameter. The number of these larger cells increased progressively until, by collection 4, a band of 6 to 8 springwood cells encompassed the narrow ring of summerwood, forming a conspicuous false ring.

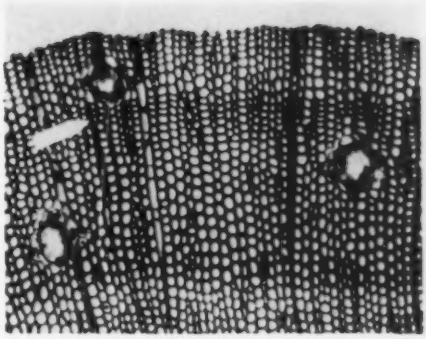

FIGURE 1. *A false ring consisting of narrow-diameter cells (arrow) produced during 3 weeks of short days, followed by large-diameter cells produced by 100 μg IAA applied to the decapitated stem tip. The effect of IAA was temporary and narrow-diameter, short-day cells are again evident near the periphery (Treatment N, Section a).*

The response in R was identical except that the false ring lay within a very wide band of large-diameter cells formed throughout the summer season (Fig. 2).

Shoot elongation of the seedlings on long days ceased early in April and a large, atypical, "loose-appearing" bud formed. After an interval of several weeks, which

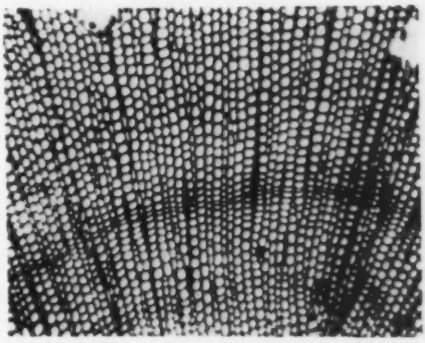

FIGURE 2. *A false ring produced by a 3-week short-day treatment followed by long-day treatment throughout the summer (Treatment R, Section a).*

FIGURE 3. *A typical "second-flush" of growth produced by long-day seedlings. On continued long days, the needles elongated to normal length and a normal-appearing bud set; in some seedlings this second bud also began growth and produced another short shoot.*

varied considerably between individual seedlings, renewed bud activity could be observed. A slight extension of the bud was followed by the appearance of needle fascicles from near the base of the bud. Additional needle fascicles appeared in the proximal region of the shoots in a manner similar to buds prematurely activated by growth substances (Duff and Nolan, 1958). After 2 to 3 weeks, the shoots had elongated 2 to 4 inches and all the needle fascicles had emerged forming tufted-appearing shoots (Fig. 3). Shortly thereafter, small, normal-appearing buds formed. Under prolonged long-day treatment (Q), new needles emerged from these buds and sporadic bud activity was noted throughout the summer.

Xylem development reflected the changes in bud activity to some extent. Beginning about April 4, shortly after elongation growth stopped in the long-day seedlings, cell wall thickness began to increase in the older sections *c* to *e*. In sections *a* and *b*, wall thickening was delayed and a slight increase was noted on April 18. By May 2, thick-walled cells were being produced in all *a* and *b* sections, but in *a* the increase was relatively slight.

In spite of the increase in wall thickness, there was no consistent change in cell diameter of the seedlings on long days. Large-diameter cells, resembling thick-walled springwood, continued to be produced at all levels in the seedlings (Fig. 4).

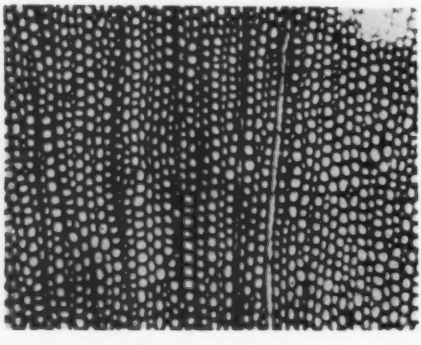

FIGURE 4. *Typical large-diameter, thick-walled summerwood produced in long-day seedlings (Treatment Q, Section c).*

In treatment Q, collected October 29, a gradual decrease in cell diameter could be noted in the outermost cell series; cambial activity was just beginning to terminate as judged by the tightness of the bark and the number of new cells visible in the cambial zone. Throughout the very wide ring in section *b* of treatments maintained on long days during the entire summer (Q and R) could be found zones of narrow-diameter cells. These varied in number from 1 to 5 in different seedlings and parts of the ring. Although no attempt was made to correlate these zones with terminal growth during the season, it is presumed that they represented periods of quiescence of the apical bud. Kramer (1957) and others have also noted that bud growth of pines on long days is intermittent. The

fact that these zones were less frequently encountered in section *a* was probably due to the sampling position, which was always located 1 cm below the bud, or, in the case of a second flush, below the original bud position.

In the older sections *d* and *e*, representing 3- and 4-year-old wood respectively, the summerwood developed in a very unusual manner. As mentioned previously, cell diameter remained large as in well-developed springwood, but the cell walls became extremely thick. For the most part, the cellular organization was quite uniform but often, in areas of rapid growth, the cells appeared somewhat disorganized and many hexagonal cells formed. The cells were quite different from reaction wood and did not resemble it in any visible manner. These cells may be likened to those found in the very high-density slash pine (*Pinus elliottii* Engelm.) of central Florida (Larson, 1957).

Reaction wood was quite common in the older sections as a result of the occasional moving of the pots in the greenhouse. A peculiar consequence of the reaction wood formed under long-day conditions was that on the side opposite, a band of narrow-diameter summerwood cells formed. This gave every appearance of a false ring but it could be readily traced around the periphery to a juncture with the reaction wood (Fig. 5).

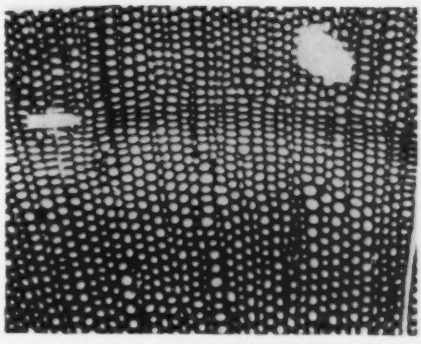

FIGURE 5. *Locally distributed zones of narrow-diameter cells were often associated with reaction wood. The reaction wood at the bottom of this photograph formed when the seedling was oriented with its vertical axis slightly tilted. The seedling overcompensated for the lean and reaction wood began forming on the side opposite; the narrow-diameter cells (arrow) were associated with this reaction wood. Vertical realignment of the stem was accompanied by the resumption of normal summerwood cell production (Treatment I, Section* d*).*

The effect of debudding on cellular growth is evident (Table 3) from the progressive decrease in the mean radial diameters of the cells in section *a*. Seedlings debudded but retained on long days, treatment S, presented an entirely different pattern of cellular development from those with buds intact, treatment I. The first two collections were similar to I but by col-

TABLE 3. Mean number and radial diameter of cells in stem section a *produced following debudding.*

Experiment	Pretreatment	Treatment	Collection number and days after treatment					
			2 (14)		3 (21)		4 (28)	
			No.	Dia.	No.	Dia.	No.	Dia.
				Microns		*Microns*		*Microns*
I[1]	Long-day	Long-day	5.0	17.4	5.0	16.1	5.0	16.8
J[1]	Short-day	Short-day	5.0	12.0	5.0	9.5	5.0	8.8
S	Long-day	Long-day, debud	2.3	16.0	4.0	15.3	5.7	12.0
T	Long-day	Short-day, debud	3.0	12.4	4.3	10.0	5.3	9.4

[1]Treatments I and J, mean values for 5 outermost mature cells.

lection 3, cell diameter began to decrease in sections *a* and *b*. By collection 4, the decrease in cell diameter had extended to section *c* and was evident to a lesser degree in *d* and *e*. The time of decapitation could again be traced by the dark-stained ring of cells.

Long-day seedlings placed on short days following debudding (T) showed an immediate reduction in cell diameter when compared with seedlings continued on long days (I and S). The resultant cell size of these seedlings (T) was very similar to that of seedlings with bud intact but given a 3-week short-day pretreatment (J).

Long-day exposure following short-day pretreatment, then debudding, treatment U, did not elicit a renewed production of springwood cells as was evidenced in a similar treatment (K) with bud intact.

Discussion

A regulatory effect of the bud on cellular development is evident from the results of this study. Continuous cambial activity with the production of large, springwood-like cells in long-day plants, suggests a rather high level of continuous meristematic activity within the growing point. Zones of narrow-diameter cells, interspersed within the ring in treatments maintained on long-day conditions throughout the summer, presumably resulted from the more or less quiescent periods following the intermittent spurts of growth.

A similar, but more pronounced, reduction in cell diameter was brought about by a sudden shift from long-day to short-day conditions. In Experiment 1 (treatment B), the reduction was gradual with a considerable period of lag following the change in daylength, while in Experiment 2 (treatment J), the reduction was relatively rapid. The differences lay in the stage of apical bud and needle development at the time of initial short-day exposure. Active shoot and needle elongation was still in progress when seedlings of treatment B were placed on short days, and some time elapsed before such growth abated. On the contrary, terminal elongation had ceased and buds had set when seedlings of treatment J were placed on short days and the adjustment interval was thus shortened. Long-day conditions following short days brought about a resumption of apical activity and an almost immediate production of large-diameter cells as evidenced by the conspicuous false rings in treatments K and R.

The necessity of the bud in maintaining the continued production of large-diameter cells was even more strikingly apparent in the decapitated and debudded seedlings. Decapitation during the active elongation stage resulted in an abrupt decrease in cell diameter (H) as opposed to the gradual reduction in similarly treated seedlings with buds intact (B). Debudding during the quiescent interval following the first bud set resulted in a reduction in cell size in seedlings maintained on long days (S) and an even more pronounced reduction in seedlings placed on short days (T) (Table 3). Resumption of long-day conditions following short-day exposure failed to revive large-diameter cell production in debudded trees (U).

The foregoing summarization illustrates the regulatory effect of the bud or elongating shoot on xylem development but gives little indication of the physiological mechanism. A highly suggestive basis of interpretation may be obtained from the results of the tip-application treatments. IAA, at a 100 μg concentration, induced production of larger-diameter cells in both experiments; 50 μg IAA was less effective. In subsequent tests, which were not a part of this experiment, applications of 500 μg and 1000 μg IAA produced extremely wide bands of large-diameter cells following decapitation and treatment.

From these results, it appears that the regulation of cell diameter may be hormonal in nature, presumably an auxin originating in the bud or growing shoot. High auxin synthesis in the apical meristem will, therefore, perpetuate the production of large-diameter cells and any factor that causes a marked reduction in apical activity,

hence auxin synthesis, will concomitantly reduce cell diameter. Short days and decapitation were both effective in this respect. As mentioned previously, delayed formation of narrow-diameter cells in short-day treatments (Experiment 1) was probably due to the high state of apical activity and auxin production of the seedlings at this stage of development; later short-day treatment (Experiment 2) showed an almost immediate response. Decapitation and debudding, which represent drastic curtailment of both apical activity and auxin production, also resulted in an immediate reduction of cell diameter.

The formation of false rings illustrates the growth correlations involved in xylem development. Short-day treatment, with its reduced auxin synthesis, effectively reduced cell diameter whereas a return to long days caused a resumption of large-diameter cell production, but only if the apical bud were left intact. Long days were, therefore, ineffective without an intact bud. On the other hand, substitution of exogenous IAA for the bud of decapitated seedlings produced similar false rings in seedlings maintained under short-day conditions. The decrease in auxin production under short-day conditions is not entirely without substantiation. Nitsch (1957) and Kawase and Nitsch (1958) have demonstrated such a reduction accompanied by an increase in inhibitor content in woody plants following a 1- to 2-week short-day exposure. Preliminary tests by the author, utilizing chromatography and bioassay, have shown a similar trend. On the basis of these tests, reference to a decrease in auxin synthesis following short-day treatment presumes an increase in growth inhibitor content.

Since the auxin stimulus presumably originates in the bud, the cellular pattern conditioned by this bud should originate basipetally to it. The extent to which this basipetal stimulus is propagated down the stem should be dependent upon the intensity of the stimulus. Thus, the exogenous IAA applications, being of relatively low concentration intensity and of short duration, were evident only in a short section of the internode beneath the point of decapitation. Similarly, in seedlings placed on long days following short days, the new large-diameter cells were first observed in the apical sections and became visible in the lower stem parts only in later collections. The zones of variable cell size in the apical sections of long-day seedlings may also represent periods of auxin deficiency associated with the intermittent growth of the terminal meristem. In a similar manner, a localized deflection, gravitational or otherwise, of the basipetal auxin stimulus could conceivably account for the narrow-diameter cells on the side opposite reaction wood (Fig. 5).

In mature trees and saplings, the hypothesis applies equally well. False rings are of common occurrence within the crown portion of many trees but only under exceptional circumstances do they reach the stem base. Generally, renewed extension growth, "second flushes," are much less vigorous than the initial spring growth and are not of sufficient intensity to stimulate a basipetal progression of springwood cells that can reach all parts of the stem. The author has noted that in slash pine the multinodal growth habit produces numerous false rings in the juvenile portion of the crown but these same false rings rarely, if ever, progress below the crown base. Jost (1893) and Kühns (1910) have reported similar instances where false rings of limited extent were actually associated with the resumption of terminal growth under experimental conditions. The failure of many investigators to note a relationship between renewed extension growth and false rings may be due to sampling the base of the tree rather than the crown portion where such ring features occur.

The data of this study also lend support to a conclusion previously reached by Priestley and Scott (1936) that summerwood formation, like that of springwood, is initiated in the bud; Wareing and Rob-

erts (1956) found that summerwood formation was associated with the mature leaves in *Robinia*. To resolve this question, one must first distinguish between the anatomical and physiological initiation of summerwood.

Anatomically, narrow-diameter cells were first observed in the apical sections and somewhat later in the older sections of decapitated and debudded seedlings, whereas the reverse was true in seedlings with bud intact. Physiologically, the factors initiating summerwood must be related to bud activity regardless of treatment. It has been demonstrated that large-diameter, springwood-like cells will be produced during periods of high growth activity and auxin synthesis. Summerwood-like cells, with narrow radial diameters, will then be produced when elongation growth terminates and the auxin content diminishes.

Since activity of the apical meristem does not entirely cease with the termination of elongation growth and bud set, some auxin will continue to be produced, except in those treatments involving decapitation or debudding. Thus, in regions of so-called "juvenile wood" (Rendle, 1958) in the vicinity of the stem apex, true summerwood will seldom form. But with increasing distance down the stem, cell diameters will decrease as auxin becomes more limiting. The rather abrupt springwood-summerwood transition in the mature wood of some older trees suggests that auxin-induced cell enlargement may be mediated by a growth-inhibiting system that becomes more prominently active following the cessation of terminal growth.

Changes in thickness of the cell walls did not necessarily parallel the variations in cell diameter. Wall thickness began increasing in the older sections (*c* to *e*) of the seedlings on long days shortly after the termination of height growth. One to several weeks later perceptible changes in wall thickness were noticeable in the *a* and *b* sections, but the transition was erratic between individual seedlings. In section *a*, the increase in wall thickness, although perceptible, was very slight while in the older sections, particularly *d* and *e*, extremely thick-walled cells were produced during the later part of the study.

In seedlings with the bud intact, prolonged short-day conditions in excess of 3 weeks generally brought about a marked increase in wall thickness throughout the seedling. Under shorter exposures to short days, such as the pretreatment period prior to decapitation, many seedlings produced cells in the *a* section with narrow diameters but thin walls; Phillips (1954) has produced similar unlignified cells in ash by an artificial dark period. As a general rule, it appeared that the first narrow-diameter cells produced on short days were comparable in wall thickness to the large-diameter cells produced prior to short-day exposure. Since the transition to thicker-walled cells in the *a* section was extremely inconsistent between seedlings, the previous long-day cells may have been either thick- or thin-walled. Invariably, wall thickness decreased following decapitation or debudding.

Because of variations in the patterns of cell-diameter and cell-wall development, it is assumed that each is dependent upon different physiological conditions for the initiation of change. Such conditions may or may not occur simultaneously. In mature wood an increase in wall thickness normally accompanies the decrease in cell diameter, while in the juvenile wood near the stem apex the cells most frequently remain thin-walled. Although auxin may also perform a role in cell wall thickening, it is believed to be more indirect and of less significance. The products of photosynthesis are more likely involved in this phase of summerwood development, and this would provide a basis for conditional acceptance of the "nutritional" theory.

The terms springwood and summerwood have been used sparingly throughout this paper with preference given to the descriptive terms large-diameter and narrow-diameter cells, respectively. This anomalous terminology has been intentionally employed

because of the atypical anatomy of juvenile wood. No known criteria will satisfactorily distinguish springwood from summerwood in the juvenile rings within the central core of a tree. Mork's (1928) criterion, which defines summerwood as all cells in which two times the double radial wall thickness is equal to or greater than the lumen, may hold true in most cases for mature wood but not for juvenile wood. In this study, cell diameter often decreased to a point where the lumen was but a thin, slit-like opening, yet cell wall thickness remained unchanged from that of the previous springwood. On the other hand, cell wall thickness often increased to a point where the lumen consisted of but a small, aperture-like opening, yet cell diameter remained unchanged from that of the previous springwood. Both of these cases could be defined as summerwood. Nevertheless, the two cell types were quite different in both their anatomical structure and physiological development. Springwood and summerwood remain as good descriptive terms so long as the limitations of their arbitrarily defined criteria are fully understood.

Summary and Conclusions

Seedlings grown under long-day conditions continued to produce springwood-like cells for an extended period of time. Summerwood-like cells could be induced to form either by short-day treatment or by decapitation. When seedlings were transferred from short-day to long-day conditions, springwood-like cell production was resumed, but only in seedlings with an intact bud. Limited production of springwood-like cells was induced in decapitated, short-day seedlings by the exogenous application of IAA.

Based on the experimental evidence of this investigation, the original hypothesis may be restated in more specific terms: Large-diameter, springwood cells will be produced during the period of active elongation growth and high auxin synthesis. Narrow-diameter, summerwood cells will be produced following the cessation of terminal growth and the consequent reduction in auxin synthesis; a growth-inhibiting system may also become more prominently active at this time. Any factor that causes terminal elongation growth to begin prematurely or to cease will bring about a respective increase or decrease in cell diameter. The extent to which a change in terminal activity will register a concomitant change in xylem tracheid development will be dependent upon the intensity of the apical stimulus. Thus, a false ring originating from a "second flush" of growth may be evident only in the uppermost parts of the stem. The increase in summerwood cell wall thickness is due to a physiological process separate from that causing the decrease in cell diameter, although the two phenomena occur more or less simultaneously in normal summerwood development. A number of questionable aspects of this hypothesis are now being investigated.

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A Statistical Investigation of Factors Affecting the Market for Hardwood Flooring

BY
G. ROBINSON GREGORY

THE PAST DECADE has seen substantial progress in empirical economic research, particularly in demand analysis. Here, the early statistical work of Schultz (1938) has not only been extended to new product areas but has also been greatly refined from a methodological standpoint. Coincident with this development in economic research has been a heightened concern by the forestry profession with the demand for forest products—a concern stimulated by the steady attrition of lumber markets, and perhaps even more by the emphasis placed on market prediction by publications such as the reappraisal reports (U. S. Forest Service 1946), the Stanford study (Stanford Research Institute 1954), and the recent Timber Resources Review (U. S. Forest Service 1958). From a purely practical standpoint it seems obvious that, since decisions made today will strongly influence the quantity of wood available to meet future demands, methods for better estimating these future demands are highly desirable.

Viewed broadly, this study is to serve as one unit in a long-term research project devoted to studying the demand for hardwood lumber and stumpage. From a narrow viewpoint, the study was instituted primarily to see if some of the techniques developed by economists in other fields might be applicable to forest product demand analysis. And there is room for considerable question here as most demand studies have been concerned with consumer goods, while the great bulk of forest products are producer goods. Hardwood and softwood construction lumber, furniture stock, pulpwood, poles, piling, hardboard, plywood—in fact most forest products—are of this latter type. Moreover, in contrast to wheat, beef, sugar, or even automobiles, forest products tend to be extremely heterogeneous. Lumber, with its many species, size, and grade differences, is a prime example. In a study of lumber "requirements" Vaux (1950) partially met the difficulty posed by heterogeneity by confining his attention to construction lumber used in California residential housing. Holland (1955), in developing a two-equation "shock" model of the demand for softwood construction lumber in the United States, also found product specification a real problem.

This characteristic heterogeneity of forest products was a major influence in deciding upon hardwood flooring as a basis for the present study. Moreover, this product provided an excellent starting point for an overall analysis of hardwood demand, since flooring has accounted for 17-½ to 26 percent of all hardwood used in manufacture during the recent past (Merrick 1951). Finally, (and perhaps most important) was the very practical consideration that early exploratory work disclosed reasonably good data, available on a monthly, quarterly, and yearly basis.

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The Hardwood Flooring Industry

As a first step in the study some two weeks were spent interviewing flooring manufacturers, trade association executives, and others in an effort to become reasonably familiar with the industry. Particular effort was directed to determining the flow of material through the production process and through market channels, and to an attempt to discover the factors believed by managers to be important in planning output programs.

Figure 1 illustrates the flow of material through the manufacturing process to the ultimate consumer. Obviously the variation in market channels is large and has increased considerably with the advent of large-scale housing developments during the post-war years. Prior to World War II much of the flooring went from producer to wholesaler to the retail lumber yard to the construction site of the single residence being built by a particular contractor. Today a single contractor may develop a tract of two or three hundred, or even two or three thousand, residential units. This contractor may deal directly with the mill for the required flooring. In some localities he may specialize even further by contracting all flooring work to a flooring contractor specializing in laying floors, who in turn contracts directly with the mill for his raw material.

The flooring market is also subject to marked regional variability. During the 1920's, for example, maple flooring comprised as much as 20 to 25 percent of the total flooring. Today less than 2 percent of

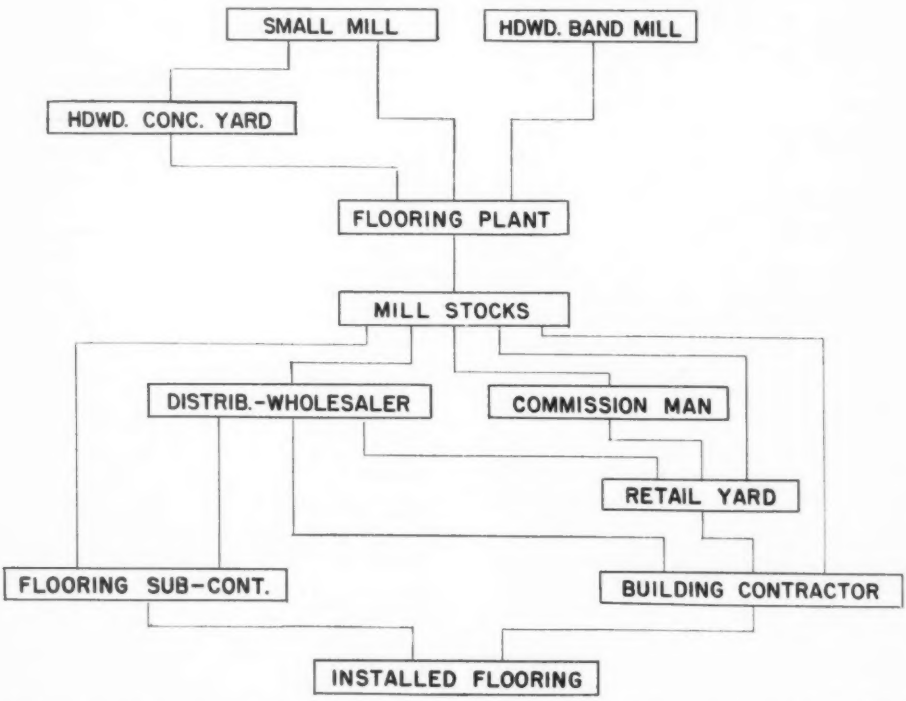

FIGURE 1. *Market flow chart for red-oak flooring, tracing the usual flow of material from initial purchase to final installation.*

the flooring used in residential construction is maple—nearly all hardwood floors are of red oak. Yet some areas have not followed this national trend. The Louisville area, for example, reportedly uses a substantial portion of white oak, while beech and pecan are favored in some localities. Even sizes vary regionally. Approximately 80 percent of the flooring sold is 2-¼ inches x 25/32 inches in size, yet one area in the North Central states uses almost nothing but 1-½ inch strips, while a far-western area reportedly uses substantial quantities of 2-inch strips that are surface nailed. Such local preferences, coupled with marked regional variation in housing style, make obvious the fact that the flooring market itself is far from homogeneous.

Nor is variation confined to demand factors; supply conditions are far from uniform. At least two, and possibly three types of flooring producers can be distinguished. First is the manufacturer who produces or buys (usually both) the raw material and converts it into flooring. These are the manufacturers whose prime business is to make and sell flooring. Second is the rather large group of hardwood lumber producers who manufacture and sell flooring primarily as a means of moving low-grade oak lumber. Examples of both are common throughout the flooring production area. Reflection on the part of the reader will confirm that these two types of producers will often respond differently to a particular set of conditions.[1]

The most important factor in establishing production schedules was believed by the majority of producers to be that of new residential construction. They stated that price of flooring was relatively unimportant in planning output, and that raw material cost, although making up nearly 70 percent of total flooring production costs, was not thought to affect production planning. Similarly, the level of mill stocks, although admitedly watched carefully, was not rated as significant in planning output. A few producers, however, were careful to qualify statements about mill stocks, observing that the more recent entrants to flooring production had experienced only the rising phase of the housing boom. Such companies were unlikely to have substantial storage space, and might well be worried by mill stocks that older producers would term "normal."

Preliminary Research

To test the importance of new construction to the flooring market, time series of annual shipments of both oak, and of maple, beech, and birch flooring, and of the number of new private dwelling units started were utilized, the data covering the period 1927-1956, excluding the war years. The ratio of multiple family units to total dwelling units started was included as a second independent variable, and the three series subjected to a multiple correlation analysis. This resulted in the equation:

$$S = 28.035 + \underset{(.131)}{.968X_1} + \underset{(.0102)}{.00941X_2}$$

where S = annual shipments of flooring (in millions of board feet).
X_1 = number of new private dwelling units started (in thousands).
X_2 = ratio of multi-family dwellings to total dwelling units started.

The multiple correlation coefficient (or $\bar{R}^2$) was .94. From these results it is obvious that the number of housing starts has indeed been an important factor, while the ratio of multi-family dwelling units to total dwelling units has not.

Similar tests were made, sometimes using annual, sometimes using monthly data—and often both—in an effort to determine the influence of the price of substitute materials on the price, production, and sale of red oak flooring. Asphalt tile and soft floor covering were both tested, but neither was found to bear a significant price, pro-

[1]A third possibility exists—the producer whose major interest is in pine, but who produces hardwood as a necessary byproduct to pine manufacture and converts the lower grades to flooring.

duction, or consumption relationship to red oak flooring. Actually, oak flooring is remarkably free from direct competitors. Asphalt tile, with an installed price per square foot of 1/6 to 1/10 that of oak flooring, is not a substitute for hardwood flooring, but rather is used (a) for floor areas not suited to oak, such as basement rooms, recreation rooms, etc., (b) in types of construction where hardwood floors are difficult to install, such as structures utilizing a slab foundation, or (c) in low-cost housing where oak floors would not be considered. An interesting sidelight was cast by the statistical analysis, however, since the difference in competitive structure of the two markets (hardwood flooring, and asphalt or rubber-tiled flooring) is immediately obvious from comparative price movements. The wholesale price index of the latter is nothing short of remarkable in its stability, especially when contrasted with the month-to-month fluctuation in prices of oak flooring.

Holland's work (1955) had established reasonably well the importance of changing population, of national income, and others of the more usual economic variables, to the consumption of forest products, while the above-mentioned preliminary research had confirmed the dependence of oak flooring markets on new residential construction. Moreover, it was obvious that the market structure following World War II had changed substantially. It was decided, therefore, to concentrate attention on the postwar period and to attempt quantification of some of the short run factors. By exercising some judgment in the selection of post-war periods, it was believed that trends might also be revealed.

Period of Analysis

In accordance with the above, three periods were selected for analysis and monthly data were used as the primary basis of the study: January 1947 through June of 1950; January 1952 through December 1955; and January 1956 through January 1958 (the most recent month for which data were then available). The July 1950 through December 1951 period was omitted because of the possible influence of the Korean War. Several models were constructed, using both seasonally adjusted, and non-adjusted data and testing different variables. All in all, approximately 75 multiple regressions were tested. While the results yielded by these analyses were both interesting and instructive, only the final periodic formulation will be reported here.

The Model

The final model represents a considerable departure from the usual econometric formulation. Technically, it is a recursive model of the type originally described and advocated by H. Wold (1956, and with Jureen, 1953). In this type of model, demand is treated in one equation, supply in another, and price in a third. The demand equation treats consumption of the product as a function of variables generated by the consumer's side of the economy; the supply equation is formed by viewing production as a function of those variables affecting the producer's decision as to the quantity of product he is to produce; and price is considered as the equilibrating factor—the factor which brings demand and supply into balance in the market place.

It is the treatment of the price function which sets this model apart from the more usual simultaneous equation approach. The latter usually regards price as simultaneously formed by the interaction of demand and supply forces; the recursive approach treats price as a dependent variable, variations in which arise because of dis-equilibrium between consumption on the one hand and production on the other. This latter view of price is, of course, in full accord with traditional economic theory. Compared with the more usual "shock" model, this formulation is relatively simple—one of the real advantages possessed by the recursive approach. The recursive nature of the model stems from its employment of lagged variables and is illustrated by the arrow diagram of Figure 2.

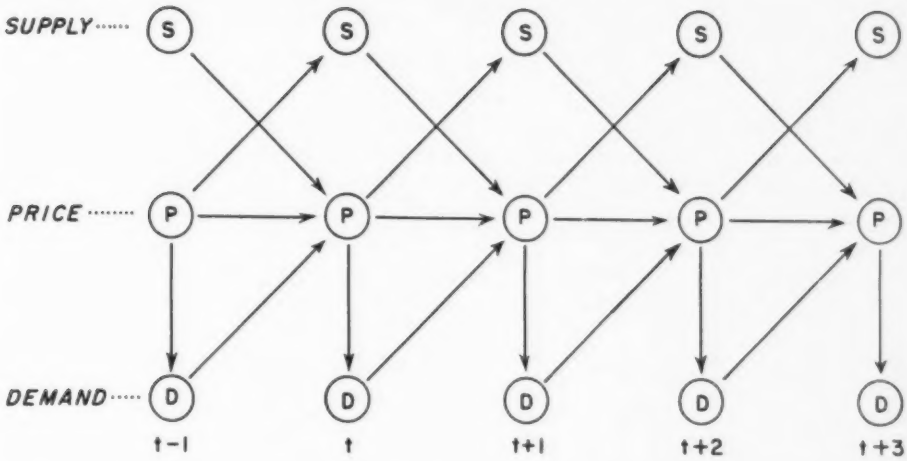

FIGURE 2. *Arrow diagram demonstrating the recursive nature of the model used in the study.*

The model itself consisted of the following equations:

The *demand* equation

$$D = a + b_1X_1 + b_2X_2 + b_3X_3$$

where

D = monthly shipments of red oak flooring (in millions of bd. ft.)

X_1 = the number of permanent nonfarm dwelling units started during the month (in thousands)

X_2 = the average construction cost of new private one-family dwelling units started, deflated by the consumer's price index, expressed in 100's of dollars

X_3 = the wholesale price index of red oak flooring, deflated by the consumer's price index.

The *supply* equation

$$S = a' + b'_1X'_1 + b'_3X'_3 + b'_4X'_4$$

where

S = monthly production of red oak flooring (in millions of bd. ft)

$X'_1 = X_1$ of the demand equation

X'_3 = the deflated wholesale price index of red oak flooring, lagged one month

X'_4 = the wholesale price index of red oak No. 1 lumber, deflated by the consumer's price index, and lagged one month.

The *price* equation

$$P = a'' + P_{-1} + b''_5X''_5 + b''_6X''_6 + b''_7X''_7$$

where

P = wholesale price index of red oak flooring, deflated by C.P.I.

P_{-1} = wholesale price index of red oak flooring, deflated by C.P.I. and lagged one month

$X''_5 = (S_{-1} - D_{-1})$, or the difference between last month's production and shipments

X''_6 = the absolute level of mill stocks, lagged one month (in millions of board feet)

X''_7 = the change in wholesale price index of red oak lumber, deflated by the consumer's price index.

Like most models of this type, these equations can be fitted by the least squares technique. The equations for each of the three periods and for all periods combined, together with the standard error of the parameters and the relevant multiple correlation coefficients, are given in Table 1.

TABLE 1. Results of fitting monthly data to the model.

Equation type and period	Resulting least squares equation[1]						R^2
			DEMAND				
Jan. '47-June '50	$D = -61.086$	$+ .159X_1$	$+ 1.833X_2$	$- .248X_3$			.83
		(.051)	(.292)	(.148)			
Jan. '52-Dec. '55	$D = -25.836$	$+ .312X_1$	$+ .973X_2$	$- .052X_3$			.83
		(.046)	(.189)	(.176)			
Jan. '56-Jan. '58	$D = 15.331$	$+ .383X_1$	$- .389X_2$	$+ .697X_3$			.82
		(.089)	(.614)	(.172)			
Summary equation	$D = 36.306$	$+ .422X_1$	$+ .493X_2$	$+ .312X_3$			.75
		(.042)	(.071)	(.124)			
			SUPPLY				
Jan. '47-June '50	$S = 2.399$	$+ .277X'_1$	$+ 1.088X'_3$	$- .696X'_4$			.64
		(.047)	(.276)	(.210)			
Jan. '52-Dec. '55	$S = 33.975$	$+ .216x'_1$	$+ 1.318X'_3$	$- 1.069X'_4$			.81
		(.044)	(.143)	(.176)			
Jan. '56-Jan. '58	$S = -23.915$	$+ .228X'_1$	$+ .142X'_3$	$+ .780X'_4$			.80
		(.082)	(.669)	(.564)			
Summary equation	$S = - 16.751$	$+ .339X'_1$	$+ 1.435X'_3$	$- .854X'_4$			.70
		(.007)	(.025)	(.021)			
			PRICE				
Jan. '47-June '50	$P = P_{-1} + 1.212$	$- .174X''_5$	$- .0223X''_6$	$+ .362X''_7$			.40
		(.089)	(.016)	(.097)			
Jan. '52-Dec. '55	$P = P_{-1} + 1.97$	$- .155X''_5$	$- .030X''_6$	$+ .232X''_7$			.42
		(.044)	(.143)	(.176)			
Jan. '56-Jan. '58	$P = P_{-1} + 1.911$	$- .055X''_5$	$- .0290X''_6$	$+ .110X''_7$			.20
		(.055)	(.018)	(.152)			
Summary equation	$P = P_{-1} + 1.192$	$- .128X''_5$	$- .019X''_6$	$+ .313X''_7$			.40
		(.035)	(.005)	(.059)			

[1]The standard errors of the regression coefficients are given in parentheses under each coefficient. For an explanation of the symbols used see text under subhead "The Model".

Results

In order that the reader might have a better idea of the fit obtained, Figure 3 is presented. Examination of the graphs will confirm that the model fits the data quite closely.

Demand. Probably the most interesting results of the study are those which follow from a comparison of the three periods analyzed. The first period (January 1947 through June 1950) was characterized on the demand side by a rapidly rising construction rate (although it included the brief recession of 1949) and on the supply side by an abnormally low level of reserve materials. In the demand equation, both number of new construction starts (X_1) and average cost (X_2) were highly significant variables, and both were positively associated with demand for flooring. The positive nature of the new housing starts is obvious—the more houses built the more flooring should be consumed—but the relationship between average construction cost and flooring sales is less clear. This variable was included in an effort to account for changing size of the average residence. Actually, at least two factors might be involved: first, as house size increases, average construction cost could be expected to rise (recall that this construction cost is deflated so that the changing value of the dollar

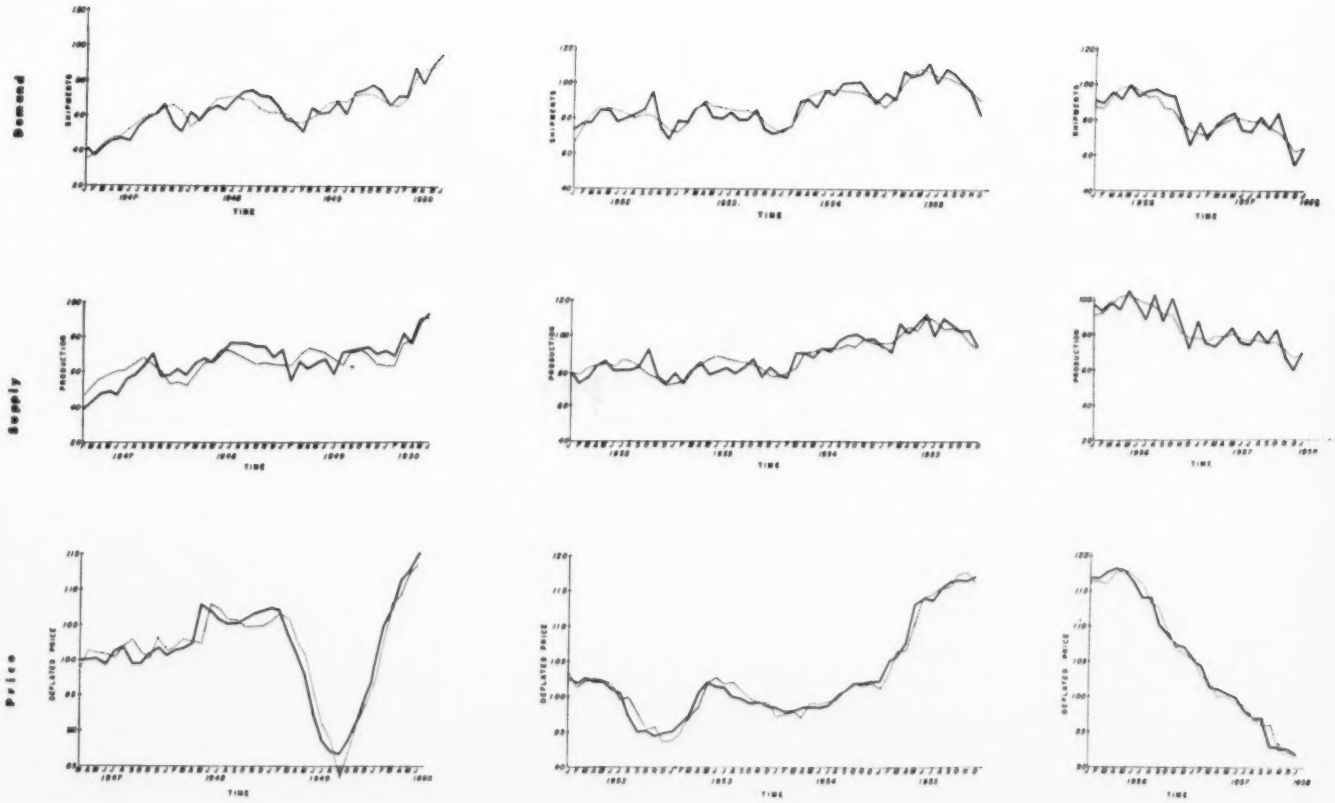

FIGURE 3. *Graphic comparison of observed red oak flooring demand, supply, and price (shipments, production, and deflated price) with that predicted by the three sets of equations over the three time periods. Solid lines show observed data, dotted lines are result of calculations from equations of Table 1.*

should not have an important influence); second, construction cost could increase as the quality of the house increased. In either case one would anticipate a positive relationship, since if quality or size were to rise, consumption of hardwood flooring might also be expected to increase.

The wholesale price index of red oak flooring, X_3, just misses being significant at the 5 percent level—the coefficient is less than twice the standard error. The sign of this coefficient is negative as expected—as price of flooring increases, its consumption declines.

Turn now to the demand equation for the second period, January 1952 through December 1955. This period was characterized during its early portion by an intensification in the construction boom, and by a leveling off of construction at its highest rate in history during the latter part. Again, both the number of new residential housing starts and the average construction cost were positively associated with shipments of red oak flooring, and both of these variables proved to be highly significant. The coefficient for X_2 (average construction cost), however, is only about half as large as it was in the former period. During this period the weight given to construction cost, whether this be a reflection of house size or quality, is considerably less than that of the former period. On the other hand, the regression coefficient for the X_1 variable has increased—in fact, almost doubled — thus giving considerably more weight to the very important variable of new residential construction. The sign of the price coefficient is again negative, but its standard error is nearly three times as large as the coefficient itself so little significance can be attached to price as a factor influencing consumption during this period.

The period January 1956 through January 1958 was characterized by an almost constant, steady decline in the construction industry. The coefficient for X_2 is decreased greatly in size—in fact, becomes negative—but is no longer significant; its standard error is nearly twice as large as the coefficient itself. Apparently for the period 1956 through 1958, size or quality (at least as reflected in average construction cost) was of no significance on the demand side. During this period, however, the coefficient for the price of red oak flooring was highly significant. Its positive nature probably stems from the fact that this was a period of decline in the construction industry; both shipments and price were declining at a steady rate throughout the entire period. Because the decline in both was so uniform, a positive correlation should be anticipated, and actually did result.

Supply. Turning now to the supply equations, the interviews with officials of the flooring industry revealed that those in decision-making positions watched construction trends extremely closely. Inclusion of this variable on the supply side, and with no lag, is justified as follows. Since the decision-makers of the flooring industry follow construction changes so very closely, it was desirable to have some indication of producers' anticipations in the supply equations. Ideally, producers' estimates of the current month's construction activity should be used, but these were impossible to obtain. The assumption made here is simply that producers' estimates of new construction are without error—that is, the actual number of new housing starts was substituted for the producer's estimate of the number of new housing starts.

During the first period the number of new housing starts (X'_1) was, as anticipated, highly significant. The coefficient of X_3, the price of red oak flooring, is positive and is highly significant, signifying that with higher prices producers tend to produce greater quantities. The coefficient of X_4, price of red oak lumber, is negative and is also highly significant for this period. This also follows what economic theory would predict: as the cost of production increases, the quantity produced tends to go down.

During the second period all three vari-

ables were again highly significant and, with the exception of the X_4 variable, of approximately the same size as those obtained for period one. The coefficient for the X_4 variable, however, increased by nearly two-thirds while its standard error decreased. As a partial explanation one might argue that, during periods of relatively stable demand, producers become more conscious of production cost factors. Conversely, when faced with a booming demand, as in the first period, cost factors would be accorded less weight in production decisions. If this were true, one would anticipate results approximating those actually obtained.

For the third period, January 1956 through January 1958, again the number of new housing starts (X'_1) is a highly significant and important variable, but neither the price of flooring nor the price of red oak lumber was significant to producer's decisions. Again, recalling the sustained decline in the residential construction industry characteristic of the period, this result should not be entirely unexpected.

Price. The three price equations will bear some further explanation. The model equation is repeated below to aid reference:

$$P = a + P_{-1} + b''_5X''_5 + b''_6X''_6 + b''_7X''_7$$

with P = Wholesale price index of red oak flooring, deflated by C.P.I.

P_{-1} = Wholesale price index of red oak flooring, deflated by C.P.I. and lagged one month.

$X''_5 = (S_{-1} - D_{-1})$ or the difference between last month's production and shipments.

X''_6 = the absolute level of mill stocks, lagged one month.

X''_7 = the change in wholesale price index of red oak lumber (deflated by C.P.I.).

Price here is regarded as being formed by "adjusting" the previously existing price according to the difference between the amount supplied and the amount demanded during the previous month (X''_5), the absolute level of mill stocks at the end of the previous month (X''_6), and the change in the deflated price of the raw material, red oak lumber (X''_7).[2]

In fitting the model by least squares the equation was transformed to

$$P - P_{-1} = a + b''_5X''_5 + b''_6X''_6 + b''_7X''_7.$$

The dependent variable thereby became the *change* in price of red oak flooring, while X''_5, the difference between amounts supplied and amounts demanded during the previous month, is the change in level of mill stocks.

Considerable question might be raised as to the desirability of using deflated price data here, as elsewhere, in the model. There is little question that producers, when looking at prices, seldom distinguish between "real" and "apparent" prices (treating the model as "behavioral") while few would argue that price decisions are reached on a "deflated" basis. The deflating procedure, however, aids in making inter-period comparisons and for this reason all prices were deflated by the consumer's price index.

The negative nature of the X''_5 coefficient is in full accord with economic theory, indicating that as the quantity of flooring supplied exceeds the quantity demanded (or as $S_{-1} - D_{-1}$ is positive) price will drop, and conversely, if more is demanded than is produced ($S_{-1} - D_{-1}$ is negative) price will be adjusted upward. During the first period (1947-1950) this relationship just misses being significant at the 5 percent level. It is highly significant during the second period, although the actual size of the coefficient is somewhat smaller. During the final period the coefficient is exceedingly small and its size is equalled by its standard error.

It would seem from this that during

[2]Actually, the price of red oak lumber No. 3A and No. 2 Common should have been used. Unfortunately, no price series for these grades was available, so the price index of No. 1 was substituted. It is believed, however, that a sufficiently close agreement between prices of these grades exists to make errors due to the substitution negligible.

periods when demand is increasing, price is reasonably responsive to disequilibrium between quantities supplied and demanded. When demand and production are both at relatively stable, high levels (as during the 1952-55 period) price is perhaps even more sensitive to differences between these two quantities. (The coefficient is nearly four times its standard error.) When both demand and production are declining, however, the weight given this factor is negligible.

The consistently negative sign of the X''_6 coefficient similarly confirms one's anticipation: A high level of mill stocks acts as a depressant upon price. It seems probable that the effect of mill stocks upon price would vary considerably according to their absolute level—an increase in mill stocks when stocks were high might be expected to have a decidedly different effect upon price than would an equally large increase when stocks were low. Unfortunately there seemed to be no simple way of taking this difference into account without some *a priori* knowledge of the changing influence itself. Little evidence can be drawn from the manner in which the magnitudes of the coefficients vary for they remain essentially the same throughout the three periods, as do their standard errors. There can be little doubt, however, that mill stocks are significant to pricing decisions.

The positive nature of the coefficient of X''_7 is again what one would expect: changes in product price vary directly with changing price of the raw material. The coefficient, it will be noted, declines in size throughout the three successive periods, and is highly significant during the first two. The relatively large standard error for the third period coefficient probably signifies that, under constantly declining product demand and price, relatively little weight is given (over the short run) to minor changes in factor costs, at least as long as the general trend of factor cost is downward.

In passing, it might be noted that the regression constant in all three price equations was positive and of approximately equal size. Since all price data were deflated, once might ascribe this bias toward higher prices simply as a reflection of the inherent tendency to boost, rather than to cut, product price. A more likely reason probably rests in the fact that prices were deflated by the consumer's price index, and construction materials — especially lumber —has had a post-war increase considerably in excess of that shown by this index.

In interpreting the significance of the relatively low multiple correlation coefficients obtained for these three price relationships, one must bear in mind that these equations are in terms of change, not in absolute terms as are the demand and supply functions. So far as fit is concerned, the price equations (at least for the first two periods) probably are as good or better than the demand or supply functions. The low correlation during the third period may simply reflect the fact that during constantly declining production and demand, price shading continues with little attention being paid to the factors normally influencing pricing decisions.

The summary equations. Little need be said regarding these summary equations. They are presented primarily to permit assessment of the model when fitted with data combined from three rather distinctly different periods. In all three equations all the variables proved to be statistically significant. It will be observed, however, that in both the demand and in the supply relationship the multiple correlation coefficient is lower than that obtained for the single period analyses, and this is so in spite of the fact that nearly three times the degrees of freedom were available for the test. Only in the price equation does the $\overline{R^2}$ remain as high for the combined as for the individual periods.

Other relationships. Of the many other relationships tested in this study perhaps the most interesting resulted from an attempt to quantify the relationship between the geographic region in which construction

took place and the quantity of flooring consumed. Were this possible, one might better know the effect of construction variation on flooring consumption, since types of construction do vary considerably by regions.

The basic model used here was

$$S = a + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + b_5X_5$$

where S = shipments of flooring

X_1 = number of new residential housing starts in the South

X_2 = number of new residential housing starts in the North Central Region

X_3 = number of new residential housing starts in the Northeastern Region

X_4 = number of new residential housing starts in the West

X_5 = wholesale price index of red oak flooring.

Since $X_1 + X_2 + X_3 + X_4$ necessarily equals the total number of new housing starts in the nation, and since this had proved a highly significant variable in other formulations, the model represented an attempt to partition the effect among regions.

The equation was next divided through by the total number of housing starts, resulting in

$$Y = a + b_1p_1 + b_2p_2 + b_3p_3 + b_4p_4 + b_5X'_5$$

where Y = the average quantity of flooring shipped per housing start

$p_1 \ldots\ldots p_4$ = the proportion of total housing starts ascribed to each of the four regions, and

X'_5 = red oak price index divided by the number of housing starts.

Because the four proportions necessarily add up to unity, one region was omitted from the calculation and the least squares regression technique applied. Data were available from 1954 through the first quarter of 1957 on a quarterly basis. Only one of the regression coefficients in this formulation came close to reaching significance at the 5 percent level, although the correlation coefficient was a respectable .82. It is believed that when more data are available, an approach similar to this might permit a better assessment of the influence of geographic region on use of various types of construction materials than has hitherto been possible.

Summary

A recursive model of the hardwood flooring market was fitted by the least squares technique, using monthly data series. The results indicate that the model is reasonably appropriate. If equal success should accompany efforts in the analysis of other major hardwood markets, it seems likely that a useful short-run model of hardwood demand can be constructed and quantified, although it must be granted that flooring provides a particularly promising first case.

Viewed somewhat narrowly, one might say that an experiment was made to test the hypothesis that modern econometric methods can yield significant results when applied to forest product market research. The hypothesis was substantiated.

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Genetik und Zuchtung der Waldbaume

By Ernst Rohmeder and Hans Schönbach. Paul Parey, Hamburg and Berlin. 338 pp., illus. 1959. Price: 38 DM.

Review by Jonathan W. Wright
Michigan State University

Not measuring up to the standards set by other recent German authors this book is a disappointment. The coverage of most subjects would have been perhaps nearly as complete as it is if the book had been prepared in 1950 from only the German, Danish, and Swedish literature. There are practically no references to the results of progeny trials of selected trees, or to replicated provenance tests, or to American work on species hybridization.

The 30-page chapter on population genetics was apparently written without first-hand knowledge of any of the original writings of the two leaders in the field—R. A. Fisher and Sewall Wright. This had peculiar consequences in the treatment of such a subject as differentiation in continuous populations. Differentiation in areally continuous populations is discussed and illustrated by an incorrectly copied graph published originally by Sewall Wright. But the fact that differentiation in linearly continuous populations follows a different pattern is not discussed.

In the chapter on genome mutations aneuploidy, which is of little interest to foresters, is given almost as much space as triploidy, which is of great practical importance. The only triploids discussed in detail are the original 3n aspen clones found in Sweden in the 1930's. No mention is made of further developments such as the Scandinavian and German testing of artificially produced triploids in aspen, birch, and alder, or the mass production for commercial planting of triploid aspen in Sweden and Denmark.

The chapter on experimental design sheds light on the author's face-value acceptance of data from old, unreplicated experiments. The only real statistics alluded to are a formula and a graph showing the relation between the standard error and standard deviation and a word definition of analysis of variance. There is a statement to the effect that modern experiments should be replicated but the line drawings of recommended outplanting plans are divided equally between unreplicated and replicated designs.

Meiosis in Interspecific Pine Hybrids

BY
KARL SAX

SPECIES HYBRIDS in the genus *Pinus* occasionally occur spontaneously and many artificial hybrids have been made in recent decades. Crosses have been made between many species within each of the two subgenera, but not between hard pines and soft pines. Among the soft pines Righter and Duffield (1951) obtained many F_1 hybrids, including crosses between the Himalayan white pine, *Pinus griffithii* McClelland, and our native white pine, *P. strobus* L. Wright (1959) reports 16 species hybrids from 38 species crosses between white pine species. In the species of hard pines Wright and Gabriel (1957) found that among 55 attempted crosses between species, 31 failed to set seed, but 23 hybrids, and 1 probable hybrid, were obtained.

Although there are limitations in species hybridization in *Pinus*, most of the hybrids obtained are vigorous and relatively fertile. Of the species hybrids made at the Institute of Forest Genetics at Placerville, Calif. Duffield (1952) reported that of the 10 which had flowered, none showed more than 40 to 50 percent of abnormal pollen and all produced at least 80 percent of normal seed set. In *Pinus murraybanksiana*, a hybrid between *P. contorta* Loud. and *P. banksiana* Lamb., Righter and Stockwell (1949) found 40 to 50 percent of poor pollen, but seed production equalled that of the parental species. The high seed set was attributed to natural selection of fertile pollen grains and archegonia in the process of fertilization.

A cytological study of several interspecific pine hybrids shows that meiosis is about as regular as it is in the parental species. These hybrids were made at the Arnold Arboretum 20 years ago as part of the Cabot Foundation project in forest tree breeding. Although these trees produced some female cones when 6 or 7 years old they did not produce abundant male flowers until 1959. The hybrids include one of uncertain origin in addition to crosses between *P. griffithii* and *P. strobus*, and between *P. parviflora* and *P. strobus*. Seed from the hybrid *P. holfordiana* A. B. Jacks, a cross between *P. griffithii* and *P. ayacahvite*, was sent to the Arnold Arboretum from an Irish botanical garden in 1930. The pollen parent was unknown, but Albert Johnson, from a study of the seedling in the Arnold Arboretum, decided that the pollen parent was probably *P. parviflora* Sieb. and Zucc.

The male cones were fixed in alcohol acetic for 24 hours and then transferred to 90 percent alcohol. Aceto-carmine smears provided satisfactory material for cytological studies. Camera lucida drawings were made of typical division figures of the F_1 hybrid *P. griffithii* × *P. strobus* (Figs. 1-6). The data are summarized in Table 1.

Chromosome pairing in the hybrids is usually complete, but in about 12 percent of the meiotic metaphase plates there were several univalents, but few if any more were found in *P. parviflora*—the species used as a control. However, the average

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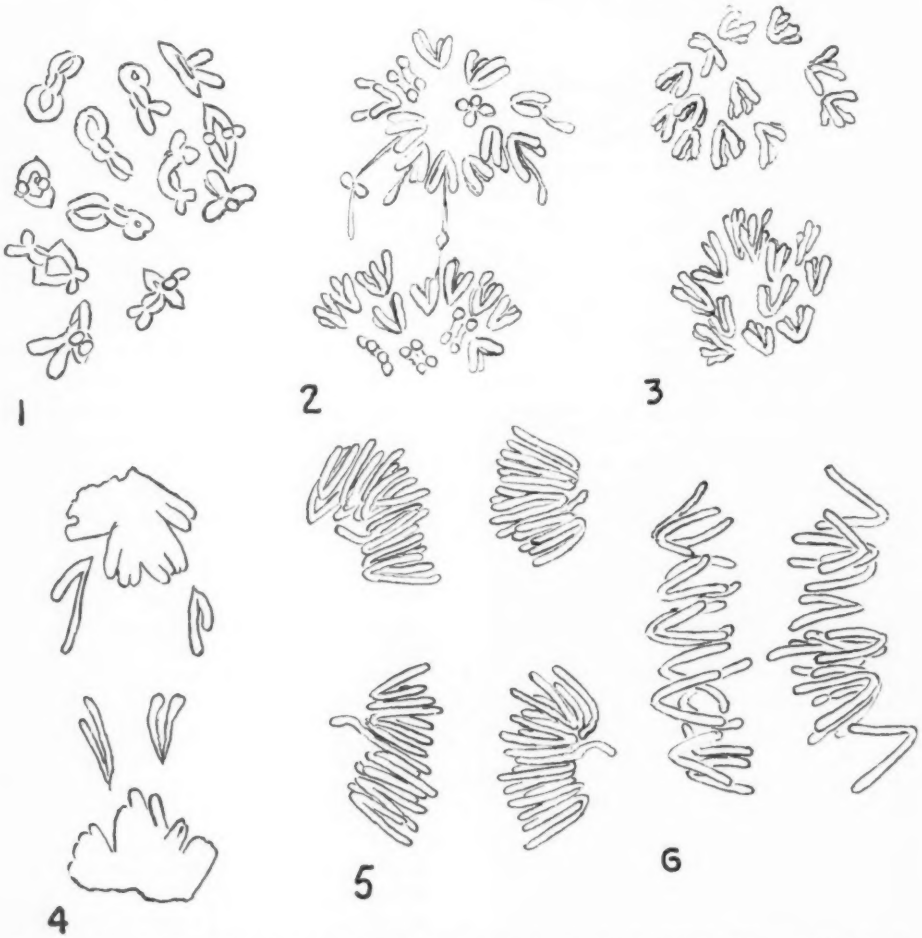
chiasma frequency of about 2.4 per bivalent (Fig. 1) was as high as we found in pine species many years ago (Sax and Sax, 1933).

The homologous chromosomes separate with difficulty, apparently due to interstial chiasmata. At early anaphase the chiasmata appear to be terminalized slowly so that the chromosome thread between the centromere and the chiasmata is stretched in a thin strand (Fig. 2). Occasionally the strand appears to have broken, which would give rise to chromosome bridges at the second meiotic anaphase as the result of the



FIGURES 1 to 6. *Camera lucida drawings of meiotic division in the F_1 hybrid* Pinus griffithii × P. strobus. (*Figs. 1-5*) *and a mitotic division in the female gametophyte* (*Fig. 6*). FIGURE 1. *Twelve bivalents at early metaphase showing high chiasma frequency.* FIGURE 2. *First anaphase with bridges caused by difficulty in terminalizing chiasmata.* FIGURE 3. *Complete separation of bivalents at late anaphase of the first meiotic division.* (*Distance between poles shortened in drawing*). FIGURE 4. *Lagging chromosomes resulting from delay in separation of bivalents.* FIGURE 5. *Second meiotic division at anaphase.* FIGURE 6. *Division of chromosomes in the female of gametophyte showing the morphology of the 12 chromosomes.*

TABLE 1. Meiotic behavior and pollen sterility in pine species and species hybrids.

Species	Meiosis								
	I Met.			I Ana.			II Ana.		
	Reg.	Irreg.	Percent	Reg.	Irreg.	Percent	Reg.	Bridge	Percent
Pinus parviflora	228	19	8	78	6	7	55	3	5
Griffithii × strobus	222	31	12	65	4	6	92	3	3
parviflora × strobus	120	17	12	23	3	12	118	3	2
Holfordiana × parviflora	200	38	12	80	6	7	80	1	1

terminal union of the ends of the broken sister chromatids. Usually, however, the bivalents eventually separate normally and 12 chromosomes pass to each pole (Fig. 3). Occasionally the terminalization of chiasmata is so long delayed that one or several chromosomes pass to the poles more slowly (Fig. 4). But at late anaphase lagging chromosomes are very rarely found.

The second meiotic division is normal (Fig. 5) with the exception of rare chromosome bridges which presumably result from chromosomes broken at first meiotic anaphase. But such bridges are no more numerous in the hybrids than they are in *P. parviflora* where about 5 percent of the second anaphase divisions are associated with a bridge.

If there is any non-disjunction of chromosomes at meiosis as the result of failure of chromosome pairing it is not evident in the chromosomes of the female gametophyte. These somatic divisions invariably involve only 12 chromosomes (Fig. 6).

Pollen sterility was based upon a count of pollen grains from anthers about to dehisce. The male flowers were brought into the laboratory and in a few hours they began to shed pollen. These pollen grains were then mounted in acetocarmine for study. In addition to obviously aborted pollen grains many were not fully differentiated and were still in the one nucleated stage. It is possible that some of these undeveloped pollen grains would not mature and function.

Although meiosis in the F_1 species hybrids is about as regular as in the parental species the degree of pollen sterility is higher. In *P. strobus* and *P. parviflora* pollen sterility was only about 5 percent as compared with 11 percent in the hybrid *P. griffithii* × *P. strobus* and 30 percent in the hybrid *P. parviflora* × *P. strobus*. In the hybrid between *P. holfordiana* and *P. parviflora* the pollen sterility was no greater than in the pure species examined.

The substantial increase in pollen sterility in some of the pine species hybrids, even when meiosis is nearly normal, does suggest that gametic sterility may be caused by incompatible genetic recombinations rather than by irregularities in meiosis.

Many crosses between pine species fail to produce seeds, even when the species belong to the same subgenus. The failure of these interspecific crosses has been attributed to the failure of the pollen tube to grow and function in the archegonium of the female flower (Buchholz, 1944). McWilliam (1959) attributes the failure of fertilization to chemical differences between the pollen and the nucellar tissue of the two species. These chemical differences may prevent normal pollen development thus preventing pollen germination or inhibiting the stimulation necessary for the development of the female gametophyte.

In at least one cross, however, fertilization occurs and seed develops, but the seeds do not germinate. Stone and Duffield (1950) found that the seeds produced by crossing *P. lambertiana* with *P. armanda*, could be induced to germinate by a modified culture technique.

If the species hybrids were heterozygous

for many chromosome inversions and translocations these structural differences should lead to meiotic irregularities. The occurrence of species hybrids with nearly normal meiotic behavior and a relatively high degree of fertility indicates that structural changes in the chromosomes have not played an important part as an isolating mechanism in speciation in the pines. The failure of many crosses to produce seed could be attributed largely to genetic differences of a chemical nature which inhibit gametic development.

The fact that relatively fertile hybrids can be obtained between such species as the Himalayan pine and our native eastern white pine, and between the Japanese white pine and our western white pine, is evidence that geographic isolation has been an important factor in speciation in the genus *Pinus*. These species maintain their identity as distinct species because of geographic isolation which prevents natural hybridization. It is remarkable that species which have been separated for perhaps millions of years are so similar in chromosome morphology and genetic constitution.

Chromosome stability and genetic compatibility are also found in other genera of the conifers. The European *Taxus baccata* L., the Asiatic *Taxus cuspidata* Sieb. and Zucc. and the American *Taxus canadensis* Marsh. are intercrossed readily and produce fertile hybrids. Fertile hybrids have also been obtained bttween the European larch, *Larix decidua* Mill., and the Japanese larch, *Larix leptolepis* Gord. (Sax and Sax, 1933). Mrs. Sax (1932) found little meiotic irregularity in the hybrid, *Larix eurolepis* Henry and an average chiasma frequency of 2.4 which was the average of the parental species. The conifers as a group show great stability in chromosome number, chromosome morphology and genetic compatibility. The fact that geographic species, which have been isolated for very long periods of time, can produce relatively fertile hybrids is of both theoretical and practical interest.

Summary

Cytological studies of F_1 hybrids between the Himalayan white pine, *Pinus griffithii*, and our native white pine, *P. strobus*; between the Japanese white pine *P. parviflora* and *P. strobus*, and between *P. holfordiana* and *P. parviflora* show that meiosis is nearly normal. The hybrids are vigorous and the fertility is relatively high. Although separated for very long periods of time the Himalayan, Japanese and American species of white pine appear to be similar in chromosome constitution and genetic compatibility.

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Testing Accuracy

BY
FRANK FREESE

CHECKING THE ACCURACY of a new estimating or measuring technique against an accepted standard is a common problem in forestry. This paper discusses the basic requirements for such a test and shows that the well-known chi-square test meets these requirements. It also points out why the t-test may be misleading when used for this purpose.

A very common example of the problem is the testing of a table to be used in estimating tree volumes in a certain area. As a standard of comparison, we might use the volumes obtained by direct scaling of felled trees. The merit of the volume table would be judged on how closely the individual tree volumes as estimated by the table correspond to the volumes given by the "standard" technique of scaling felled trees.

Another example might be the testing of some new technique for predicting volume growth. Predictions for a number of sample plots could be compared to the growth on these plots measured as the difference in plot volumes at the beginning and end of the prediction period. The utility of the new technique would depend on how closely the predicted values were to the actual growth.

There are numerous other examples of the problem: can tree heights be accurately measured by a certain hypsometer, what is the possibility of estimating seed viability by some vital stain technique, can timber volumes be estimated from measurements made on aerial photographs?

Almost inevitably the estimates made by the new technique will differ somewhat from the "true" values given by the accepted standard technique. If the difference is a constant or some mathematical function of the true value, the new technique is said to be biased. If the new technique is unbiased but gives values that fluctuate widely around the true value, it is said to lack precision. And, of course, inaccuracy may be due to both bias and lack of precision.

The first problem is to decide whether the differences, regardless of their source, can be tolerated. If they can, the new technique can be substituted for the standard. If they cannot be tolerated, the source of inaccuracy must be identified and removed or the new technique discarded.

Three elements are required in evaluating the accuracy of a technique:

(a) A statement of the accuracy required, or the inaccuracy that will be tolerated.
(b) A measure of the accuracy attained in trials of the new technique.
(c) A method of deciding whether the accuracy attained is equal to the accuracy required.

All three of these elements are provided for by the standard chi-square test of a hypothesized variance.

$$\chi^2_{(n)df} = \frac{\sum_{i=1}^{n} (x_i - \mu_i)^2}{\sigma^2}$$

where: x_i = The value of the i^{th} observational unit as estimated by the new technique.

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μ_i = The "true" value of the i^{th} observational unit as measured by the standard technique.

n = The number of units observed (i=1 . . . . n).

σ^2 = The required accuracy as described below.

The value of χ^2 as computed from observational data is compared to the tabular[1] value of χ^2 with n degrees of freedom at the desired probability level (usually .05, the 5-percent level of testing). If the computed χ^2 is greater than the corresponding tabular value, the inference is that the new technique does not provide the required accuracy.

Statement of Required Accuracy

Of the three elements essential for a sound decision the one frequently overlooked is the statement of the accuracy required if the new technique is to be considered acceptable. A volume table that gave volumes differing by 200 or 300 board feet from a scaled volume of 500 board feet would certainly be considered unacceptable for most uses. A table giving volumes to within 5 board feet of a scaled volume of 500 board feet would usually be acceptable. But what about errors of 10 feet, 30 feet, 60 feet, 100 feet? Clearly, the accuracy of an estimating or measuring technique cannot be tested until the potential users have stated what degree of accuracy will be regarded as acceptable.

In the chi-square test the accuracy requirement is specified in the form of a hypothesized variance (σ^2). If the user specifies that the technique will be acceptable if the estimated values (x_i) are within E units of the true value (μ_i) unless a 1-in-20 chance has occurred, then:

$$\sigma^2 = \frac{E^2}{(1.96)^2}$$

where 1.96 is the value of the standard normal deviate corresponding to a two-tailed probability of .05.

If the user specifies that the estimated values should be within E units of the true value unless a 1-in-100 chance has occurred, then:

$$\sigma^2 = \frac{E^2}{(2.575)^2}$$

In general, if the estimates must be within E units of the true value unless a 1-in-Z chance has occurred, then:

$$\sigma^2 = \frac{E^2}{\tau^2}$$

where τ is the value of a standard normal deviate corresponding to a probability of $\frac{1}{Z}$.

Suppose a volume table is required to estimate tree volumes to within $\pm$ 30 board feet unless a 1-in-100 chance has occurred. Then the value of σ^2 used in the computation of χ^2 would be:

$$\sigma^2 = \frac{30^2}{(2.575)^2} = 135.7338$$

Two Examples

The data in Table 1 represent hypothetical measurements (x_i) made by a procedure (Technique 1) that is being considered as a substitute for some standard procedure. The true values (μ_i), as given by the standard, are also shown. It has been specified that the substitute technique will be acceptable if it will estimate the true values to within 30 units unless a 1-in-20 chance has occurred. Translating the accuracy specification to σ^2 gives:

$$\sigma^2 = \frac{30^2}{1.96^2} = 234.2774$$

[1]Tables of the chi-square distribution can be found in most books of statistical methods. Since many tables do not give values of χ^2 for over 30 degrees of freedom, the values of χ^2 at the .05 level for 31 to 100 degrees of freedom are shown in Table 3. The table also provides a procedure for computing approximate χ^2 values at the .05 level for any number of degrees of freedom.

And computing χ^2:

$$\chi^2_{10\,df} = \frac{(-5)^2+(-20)^2+\ldots+(-10)^2}{234.2774} = 9.177.$$

If significance is to be tested at the 5-percent level, this value of χ^2 must be compared to the tabular value with 10 degrees of freedom. Since computed χ^2 is less than the tabular value of 18.31, it appears that Technique 1 will provide the required accuracy.

The data in Table 2 represent hypothetical measurements made by a procedure (Technique 2) that is obviously incapable of meeting the accuracy requirement of ± 30 units. The chi-square test gives a value of:

$$\chi^2_{10\,df} = \frac{(-80)^2+(-120)^2+\ldots+(-160)^2}{234.2774} = 589.045.$$

This value greatly exceeds the tabular value (5-percent level) of 18.31, thus confirming that Technique 2 is not accurate enough.

An Approximate Test of Accuracy After Elimination of Bias

The chi-square test will reject inaccurate techniques regardless of the source (bias, lack of precision, or both) of inaccuracy. However, as some techniques may be capable of giving excellent accuracy if bias can be removed, it is often desirable to have an indication of the accuracy after adjustment. If the bias (B) is assumed to be the same for all values of μ_i its magnitude can be estimated as the mean difference between the estimated and the standard values:

$$B = \frac{\sum_{i=1}^{n} d_i}{n} = (\bar{x} - \bar{\mu})$$

In this case, an approximate test of the bias-free precision of the new technique would be:

$$\chi^2_{(n-1)df} = \frac{\sum_{i=1}^{n}(x_i-\mu_i)^2 - nB^2}{\sigma^2}$$

TABLE 1. Technique-1 values (x_i) compared to the standard-technique values (μ_i).

Observation No.	x_i	μ_i	$d_i=(x_i-\mu_i)$
1	495	500	−5
2	360	380	−20
3	480	480	0
4	280	290	−10
5	610	600	+10
6	505	540	−35
7	320	320	0
8	390	400	−10
9	350	360	−10
10	310	320	−10
Total	4,100	4,190	−90
Mean	410	419	−9
$\sum_{i=1}^{n} d_i^2$			2,150

TABLE 2. Technique-2 values (x_i) compared to the standard-technique values (μ_i).

Observation No.	x_i	μ_i	$d_i=(x_i-\mu_i)$
1	420	500	−80
2	260	380	−120
3	540	480	+60
4	180	290	−110
5	450	600	−150
6	580	540	+40
7	430	320	+110
8	210	400	−190
9	300	360	−60
10	160	320	−160
Total	3,530	4,190	−660
Mean	353	419	−66
$\sum_{i=1}^{n} d_i^2$			138,000

Note that chi-square would, in this case, have $(n-1)$ degrees of freedom. To illustrate, the estimate of bias for Technique 2 is:

$$B = (\bar{x} - \bar{\mu}) = (353 - 419) = -66$$

Then the approximate test of the accuracy of this technique after elimination of bias is:

$$\chi^2_{9df} = \frac{138{,}000 - 10(-66)^2}{234.2774} = 403.11$$

Since this value exceeds the tabular value of χ^2 at the 5-percent level (16.92), we would infer that Technique 2 would be unable to meet our accuracy requirements even if the bias could be eliminated.

Instead of being constant, the magnitude of a bias may increase or decrease directly with the true values μ_i. In this case, an approximate test of the bias-free accuracy of a measurement technique would require fitting a linear regression of x_i on μ_i computing sum of squared residuals about this regression, and then using chi-square to test this sum of squares against the hypothesized variance (σ^2). Chi-square computed in this way will have $(n-2)$ degrees of freedom. The procedure can be summarized symbolically as follows:

$$\chi^2_{(n-2)df} = \frac{\text{Residual } \boxed{\text{SS}}}{\sigma^2}$$

where: Residual $\boxed{\text{SS}}$

$$= \left[\sum_{i=1}^{n} x_i^2 - \frac{\left(\sum_{i=1}^{n} x_i \right)^2}{n} \right]$$

$$- \frac{\left[\sum_{i=1}^{n} x_i \mu_i - \frac{\left(\sum_{i=1}^{n} x_i \right) \left(\sum_{i=1}^{n} \mu_i \right)}{n} \right]^2}{\left[\sum_{i=1}^{n} \mu_i^2 - \frac{\left(\sum_{i=1}^{n} \mu_i \right)^2}{n} \right]}$$

The formula looks more ferocious than it is. To apply it to the data for Technique 2, we will need the following individual terms:

$\sigma^2 = 234.2774$ (as before)

$n = 10$

$\sum_{i=1}^{n} x_i = 3530$

$\sum_{i=1}^{n} x_i^2 = 1{,}451{,}500$

$\sum_{i=1}^{n} x_i \mu_i = 1{,}584{,}200$

$\sum_{i=1}^{n} \mu_i = 4190$

$\sum_{i=1}^{n} \mu_i^2 = 1{,}854{,}900$

Substituting the appropriate terms in the equations we obtain:

$$\text{Residual } \boxed{\text{SS}} = \left[1{,}451{,}500 - \frac{(3530)^2}{10} \right] - \frac{\left[1{,}584{,}200 - \frac{(3530)(4190)}{10} \right]^2}{\left[1{,}854{,}900 - \frac{(4190)^2}{10} \right]}$$

$$= 205{,}410 - \frac{(105{,}130)^2}{99{,}290}$$

$$= 94{,}096.506$$

Then

$$\chi^2_{8df} = \frac{94{,}096.506}{234.2774} = 401.646$$

The tabular value of chi-square (with 8 df) at the 5-percent level is 15.51. Since the computed value is larger, we would conclude again that, even with bias eliminated, Technique 2 would not provide the required accuracy.

Expression of Error as a Percent of the True Value

Quite often accuracy requirements will be expressed in relative terms rather than in

absolute units. Instead of saying that the new technique should give values that are within 30 units of the true value, we might specify that the estimates be within P percent of the true value unless a 1-in-20 chance has occurred. Symbolically this means $E_i = \frac{P\mu_i}{100}$ and our accuracy statement expressed as a hypothesized variance would become:

$$\sigma_i^2 = \frac{E_i^2}{1.96^2} = \frac{P^2\mu_i^2}{196^2}$$

The chi-square formula would be:

$$\chi^2_{(n)df} = \sum_{i=1}^{n}\left[\frac{(x_i-\mu_i)^2}{\sigma_i^2}\right] = \sum_{i=1}^{n}\left[\frac{196^2\,(x_i-\mu_i)^2}{P^2\mu_i^2}\right] = \frac{196^2}{P^2}\sum_{i=1}^{n}\left(\frac{x_i}{\mu_i}-1\right)^2$$

In applying this test to the data in Table 1 it might be specified that the estimated values be within 5 percent of the true values unless a 1-in-20 chance has occurred. Then:

$$\chi^2_{10df} = \frac{196^2}{5^2}\times\left[\left(\frac{495}{500}-1\right)^2+\left(\frac{360}{380}-1\right)^2+\ldots+\left(\frac{310}{320}-1\right)^2\right]=16.767$$

And for Technique 2:

$$\chi^2_{10df} = \frac{196^2}{5^2}\times\left[\left(\frac{420}{500}-1\right)^2+\left(\frac{260}{380}-1\right)^2+\ldots+\left(\frac{160}{320}-1\right)^2\right]=1497.268$$

Again Technique 1 would be accepted, and Technique 2 would be rejected.

If the individual differences $d_i = (x_i - \mu_i)$ have already been computed, χ^2 can be more simply computed as:

$$\chi^2_{(n)df} = \frac{196^2}{P^2}\sum_{i=1}^{n}\left(\frac{d_i}{\mu_i}\right)^2$$

Why Not Use the t-Test?

The t-test of paired replicates is frequently used to judge a new estimating technique. For this purpose the value of t with $(n-1)$ degrees of freedom is computed as:

$$t = \frac{\bar{d}}{\sqrt{\dfrac{\sum_{i=1}^{n} d_i^2 - \dfrac{(\sum_{i=1}^{n} d_i)^2}{n}}{n(n-1)}}}$$

where: d_i = The difference between the true value of the i^{th} observational unit and the value as estimated by the new technique.

$\bar{d}$ = Average of the d_i's

n = The number of observational units.

Although the results of the t-test are not without interest, they frequently give rise to rather anomalous conclusions. This is well illustrated by the hypothetical data in Tables 1 and 2. Technique 1 (Table 1) does a good job of approximating the standard values. The differences between the estimated and standard values are small but fairly consistent; hence the standard error of the mean difference (the denominator in the formula for t) is small. Because of this small standard error, the mean difference of only 9 units is shown to be significant at the 5-percent level. Significance is generally taken as evidence that the new procedure is not accurate enough to substitute for the standard.

Technique 2 (Table 2) does not do a good job of approximating the standard values. Differences between estimated and standard values are large and erratic, leading to a large standard error of the mean difference. The size of this standard error prevents even the large mean difference

of 66 units from being significant when tested by t. Lack of significance is often accepted as evidence that the new procedure can be substituted for the standard.

Thus, the t-test as interpreted here would reject what seems to be a good technique and would fail to reject a poor technique. Paradoxically, the precision of Technique 1 has been the instrument of its demise while Technique 2 has been saved by its own lack of precision. The inconsistency is fairly obvious in this case. In most cases, this seeming betrayal of the forester's faith in the t-test is less apparent.

The failure, however, is attributable to misapplication of the test, not to any fundamental flaw in the t-test itself. When the t-test is used, the variation among the individual differences between the new technique and the standard is accepted as an inherent characteristic of the population of these differences. Using this variation (in the form of a standard error of mean difference), the t-test measures the probability that the mean difference observed could have come (via sampling error) from a population having a mean difference of zero. If this probability is .05 or less, the difference is said to be significant at the 5-percent level and the hypothesis of a zero difference is rejected. Now, if there is a real difference between the population means of two measurement techniques, one of which is assumed to give the true values, the other technique must be considered biased. Hence, one form of inaccuracy (lack of precision as indicated by variation of individual differences) is being accepted as a population characteristic and used in testing for another form (bias). This is the source of the paradox. If the variation among individual differences is small (contributing to good accuracy), even a small bias (good accuracy) may prove significant. So the fact that the method is capable of giving consistent estimates leads to rejection on the grounds of bias. If the variation among individual differences is large (contributing to poor accuracy), even a large bias (poor accuracy) may not be significant. So the inability of the technique to give good estimates leads to its acceptance even in the presence of a large bias.

A statistic which provides a measure of accuracy is the variance. The term

TABLE 3. Chi-square values at the .05 probability level for degrees of freedom 31 to 100.

df	χ^2	df	χ^2
31	44.98	66	85.96
32	46.19	67	87.11
33	47.39	68	88.25
34	48.60	69	89.39
35	49.80	70	90.53
36	50.99	71	91.67
37	52.19	72	92.81
38	53.38	73	93.94
39	54.57	74	95.08
40	55.75	75	96.21
41	56.94	76	97.35
42	58.12	77	98.48
43	59.30	78	99.61
44	60.48	79	100.75
45	61.65	80	101.88
46	62.83	81	103.01
47	64.00	82	104.14
48	65.17	83	105.26
49	66.33	84	106.39
50	67.50	85	107.52
51	68.67	86	108.65
52	69.83	87	109.77
53	70.99	88	110.90
54	72.15	89	112.02
55	73.31	90	113.14
56	74.46	91	114.27
57	75.62	92	115.39
58	76.77	93	116.51
59	77.93	94	117.63
60	79.08	95	118.75
61	80.23	96	119.87
62	81.38	97	120.99
63	82.53	98	122.11
64	83.67	99	123.22
65	84.82	100	124.34

The .05 value for χ^2 with ν df can be approximated by:

$$\chi^2_{(\nu)\text{df}} = .853 + \nu + 1.645\sqrt{2\nu - 1}$$

$\sum_{i=1}^{n} (x_i - \mu_i)^2$ provides a sample-based estimate of n times the variance of individual observations (x_i) about their expected values (μ_i). If the x_i follow a normal distribution with a mean of μ_i, the expression

$$\frac{\sum_{i=1}^{n} (x_i - \mu_i)^2}{\sigma^2}$$ follows the chi-square distribution with n degrees of freedom and permits testing the hypothesis that the sampled population has a variance of σ^2. The value of σ^2 is established, as previously described, by the accuracy requirements. The hypothesis may be rejected because the expected value of x_i is not μ_i (i.e., bias), because the variance is not σ^2 as hypothesized, or for a combination of these reasons.

Summary

Testing the accuracy of some measurement against an accepted standard requires a statement of the accuracy required, a measure of the accuracy attained, and an objective method of deciding whether the accuracy attained is equal to the accuracy required. All three requirements are met by the standard chi-square test.

Inaccuracy may be due to lack of precision, to bias, or to a combination of these. The chi-square test will reject an inaccurate technique regardless of the source of inaccuracy. However, the test can be modified to evaluate accuracy after elimination of bias.

The t-test, though commonly used, is not suitable for tests of accuracy. It uses one form of accuracy (precision) to test for the other form (freedom from bias), frequently with anomalous results.

Plants and Environment

A textbook of plant autecology. Second edition. By R. F. Daubenmire. John Wiley & Sons, Inc. New York. 422 pp. 1959. $6.95.

Review by Stephen H. Spurr
The University of Michigan

Among the texts on general plant ecology, Daubenmire's survey of autecology is particularly suitable for use in forestry schools because of the author's broad experience in the North American forest and his consequent awareness of ecological problems of interest to the forester. Daubenmire is Professor of Botany at the State College of Washington. His own investigations have contributed materially to an understanding of the ecology of the forests of the Rocky Mountains.

The text deals almost entirely with autecology, the influence of environment upon plants. The individual habitat factors of soil, water, temperature, light, atmosphere, the biota, and fire are taken up singly. This approach is clear and suitable for elementary instruction, although the complex interactions involved are necessarily not as strongly emphasized as would be desirable for a fuller understanding of the relationships between the site and the plant community. The second edition contains new material on evapotranspiration, the significance of dew, and several other topics; but the organization and material remain close to the first edition. Of particular interest are the chapters on the fire factor, and on the impact of the environment on adaptation and speciation.

Covering as it does the whole field of plant autecology, the book will seem somewhat elementary in some aspects of forest ecology. Yet, the treatment is always factual and accurate with the result that even the specialist may profit from a detailed study. In forestry training, the text may well be used in the first half of the standard upperclass course in forest ecology or silvics.

The Yeasts Associated With Bark Beetles

BY
ROBERT Z. CALLAHAM
MOSHE SHIFRINE

THE PURPOSE of this summary is threefold: (1) to bring together many scattered and inaccessible references to bark-beetle yeasts; (2) to give additional information on a recent paper on yeast taxonomy (Shifrine and Phaff, 1956); and (3) to present data on the growth of some bark-beetle yeasts at several temperatures.

Interest in the microorganisms associated with bark beetles has been stimulated by studies of the resistance of pines to bark beetles. Yeasts, one of the most commonly associated microorganisms, were first to be brought under close scrutiny. These yeasts ferment sugar in the pine phloem, and this fermentation is believed to produce attrahents for bark beetles. Bark beetles and their broods eat the infected phloem. This general situation has been known for some time (Grosmann, 1930; Person, 1931).

Some facets of this general association of yeasts and bark beetles might critically influence the susceptibility or resistance of a particular pine to a particular bark beetle. For example, a yeast could enhance susceptibility. It could produce an attrahent specific for a certain bark beetle, or it might produce nutrients otherwise unavailable to a bark beetle and its brood (Koch, 1956). Thus a yeast might determine the success or failure of insect brood development in a particular pine species. Particularly would this be so if the yeast were able or unable to utilize tissues of the pine as substrate.

The Ubiquitous Association of Yeasts With Bark Beetles

Published information about the yeasts associated with bark beetles deals chiefly with a few yeasts found with some common bark beetles (Steinhaus, 1946, 1949; Mrak and Phaff, 1948; Beal and Massey, 1945). Shifrine and Phaff (1956) review the literature on the taxonomy of these yeasts from bark beetles. But relatively little is known or has been written about the ecological interaction between bark beetles and yeasts.

Helene Grosmann (1930) apparently was the first to study the ecological relationship between bark beetles and their yeasts. Studying *Ips typographus* L. in Germany, she found that different species of *Ips* seemed to carry certain kinds of yeasts. She noted that each insect specimen had only one or occasionally two yeast forms and that the yeasts were transferred from tree to tree by the adult beetles, which inoculated the phloem of each new host. Eggs of bark beetles also were covered with yeasts. The emerging larvae ate the yeasts and carried them into the phloem. Consistently, she found yeasts in the intestinal tracts of the larvae, and less frequently in the

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This paper reports work done by the former Bureau of Entomology and Plant Quarantine in cooperation with the Forest Service until the Department of Agriculture was reorganized in 1953, and continued thereafter by the Forest Service, which now does forest insect research.

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pupae. She even found large numbers of viable yeasts in the emerging adults and in the collapsed stomachs of larvae starved for 24 hours; she took this to indicate that the yeast cells are not digested.

In Poland, Siemaszko (1939) extended her work. He found unidentified yeasts associated with *Ips typographus* attacking *Picea excelsa* Link, with *I. sexdentatus* Boern. attacking *Pinus silvestris* L., and with both *Scolytus scolytus* Fabr. and *S. multistriatus* (Marsh) attacking *Ulmus foliacea* Gilib.

Several workers in this country have recognized the consociation of yeasts with species of *Dendroctonus* and *Ips*. Person (1931) was the first. He worked with *Dendroctonus brevicomis* Lec. attacking *Pinus ponderosa* Laws. He found many yeast cells in considerable abundance, both on the integuments and in the intestinal tracts. He stated: ". . . the yeast was by far the most abundant and the only organism apparently always present on the larvae and new adults of the beetle."

Rumbold (1931) reported the isolation of yeasts from slivers of wood taken near the galleries of *Ips grandicollis* Eichh. and *I. calligraphus* Germ. attacking southern yellow pines, of *Dendroctonus brevicomis* attacking *Pinus ponderosa*, and of *D. frontalis* Zimm. attacking *P. echinata* Mill. She also found[1] yeasts associated with many other bark beetles:

Dendroctonus
- *murrayanae* in *Picea engelmannii*, *Pinus contorta*
- *piceaperda* in *Picea glauca*
- *engelmanni* in *Picea engelmannii*
- *pseudotsugae* in *Pseudotsuga menziesii* var. *glauca*
- *monticolae* in *Pinus flexilis*, *P. monticola*, *P. contorta*, *P. ponderosa*
- *ponderosae* in *Pinus ponderosa*
- *jeffreyi* in *Pinus jeffreyi*

Ips
- *oregoni* in *Pinus contorta*, *P. ponderosa*
- *pini* in *Pinus strobus*
- *avulsus* in *Pinus rigida* and *P. echinata*

Leach and his coworkers (1934) found characteristic yeasts constantly associated both internally and externally with adults of *Ips pini* Say and *I. grandicollis* attacking logs of *Pinus resinosa* Ait. The yeasts were cultured both from the adults as they alighted to attack and from the bark and sapwood adjacent to freshly made nuptial chambers. Yeasts also were cultured from the "sawdust" plugging the egg niches, from the surfaces of the eggs themselves, from the intestinal tracts of the larvae, and from newly maturing and emerging adult beetles. Yeasts were not found in the intestinal tracts of the pupae.

Caird (1935) found yeasts universally associated with *Dendroctonus frontalis* attacking *Pinus echinata*. Yeasts were not found in the sapwood internal to the outer annual ring until sapwood conduction ceased. Then yeasts were found throughout the xylem.

Rumbold (1936) reported yeasts associated with *Dendroctonus pseudotsugae* Hopk. attacking *Pseudotsuga menziesii* (Mirb.) Franco and *D. piceaperda* Hopk. attacking *Picea glauca* (Moench) Voss. Lu and his coworkers (1957) recently expanded on Rumbold's initial discovery that *D. pseudotsugae* carried "two types of yeast —Zygosaccharomycetes and an anascosporogenous mycelium-forming group."

Holst (1936) described a yeast, which had been isolated by Rumbold, as *Zygosaccharomyces pini*, now *Pichia pini* (Holst) Phaff. He gave the source of his cultures as: *Dendroctonus brevicomis* attacking *Pinus ponderosa*, *D. frontalis* attacking *P. echinata*, *D. valens* Lec. attacking *P. strobus* L. and *P. echinata*, *Ips oregoni* (Eichh.) and *I. emarginatus* Lec. attacking *P. ponderosa* and *I. avulsus* Eichh., *I. grandicollis*, and *I. calligraphus* all attacking *P. echinata*.

Bramble and Holst (1940), working with *Dendroctonus frontalis* infestations in

[1]C. T. Rumbold. Progress report of investigations in 1930 of blue-stain fungi associated with insects. Preliminary report of investigations in 1931 of blue-stain fungi associated with insects, Forest Products Laboratory, Madison, Wisc., 1931. (Typewritten reports.)

Pinus echinata, found yeasts distributed up and down the stem into the heartwood within two weeks after beetle attack. They isolated yeasts from phloem adjacent to galleries within 24 hours after attack and demonstrated through inoculation experiments that the yeasts had no effect on conduction in the xylem. Yeast-inoculated trees did not die.

Rumbold (1941) regularly isolated *Zygosaccharomyces* (*Pichia*) *pini* and anascosporous yeasts from adults of *Dendroctonus monticolae* Hopk. attacking *Pinus monticola* Dougl., *P. contorta* var. *latifolia* Engelm., and *P. flexilis* James, and from adults of *D. ponderosae* Hopk. attacking *P. ponderosa*, *P. contorta* var. *latifolia*, and *P. flexilis*.

Anderson (1948) isolated unidentified yeasts from the galleries of *Ips pini* attacking *Pinus banksiana* Lamb.

Shihata and Mrak (1952) isolated *Pullularia pullulans* and *Kloeckera lindneri* from unidentified bark beetles in southern California.

Wickerham (1956) reports a new yeast, *Hansenula wingei*, isolated from frass and an *Ips* adult taken from *Picea engelmannii*.

Are Bark Beetles and Yeasts Symbionts?

Several of these authors have speculated on the constant association of yeasts and bark beetles. Some feel it is a truly obligate symbiotic relationship. But from her work, Grosmann concluded that yeasts were not internal symbionts of the bark beetles because one larva apparently free of yeast developed successfully into a mature adult. Six other larvae reared to adults were infected with yeasts. Holst (1937) was more successful in rearing sterile bark beetles *in vitro*. The limited scope of both of these studies makes them inconclusive. One cannot determine whether the symbiosis between these two organisms is obligate. Furthermore, one must consider that the rearing of sterile adults alone does not disprove a symbiotic association. These two workers were not able to carry their work through a complete generation; hence, the suggestion that yeast-feeding could be prerequisite to fertility has not been confirmed.

In contrast to the Grosmann-Holst opinion, several other facts stand as evidence for a symbiotic relationship. (1) The two organisms have a general consociation; all species of bark beetles which have been studied have had associated yeasts. (2) Yeasts and yeast-infected phloem have attracted bark beetles in some experiments (Person, 1931; Lu *et al.*, 1957). (3) The yeasts are dependent upon the bark beetles for inoculation into new substrate. (4) Desiccation of the xylem follows the exposure of this tissue to the air in the bark-beetle galleries. The rapid development of yeasts throughout the xylem can occur only after this desiccation (Caird, 1935). Thus, the bark beetle makes available to the yeast a very large volume of xylem substrate in addition to the relatively small volume of phloem substrate. (5) Yeasts are eaten and digested by feeding larvae and adults; they also are found associated with the non-feeding egg and pupal stages.

The foregoing lines of evidence do not provide a conclusive base for proving or disproving the hypothesis of obligate symbiosis between yeasts and bark beetles. More definite evidence is needed.

Yeasts in Bark-Beetle Attraction

Person (1931) truly pioneered in directing studies of the role of yeasts in bark-beetle attraction. He tested the attractivity of many parts of ponderosa pines to *Dendroctonus brevicomis* adults. Phloem inoculated with the yeast isolated from larvae and adults was the most attractive material. He conjectured that after the yeast is inoculated into the host there is a strong attraction of bark beetles to the products of yeast fermentation. Leach and his coworkers (1934) pointed out that the yeasts "must be considered as truly symbiotic with the beetles" if Person's explanation of attraction is correct.

One prime difficulty with Person's hypothesis of attraction should be brought out.

The early work of Holst (1936) and the recent work of Shifrine and Phaff (1956) and of Lu *et al.* (1957) showed that the yeasts from bark beetles have only a *weak* capacity to ferment monosaccharides. Thus, actually only very little attrahent may be produced by fermentation. Anderson's (1948) work also provides another possible contradiction to the hypothesis of attraction to a product of fermentation. The yeasts he cultured from *Ips pini* did not produce an attrahent for that bark beetle.

Considerable unpublished work is available to indicate that yeast-inoculated phloem is attractive to bark beetles. Mirov,[2] working for Person, made the initial discovery. He allowed pine phloem to stand in water with water and airborne microorganisms. This phloem was more attractive to adults of *Dendroctonus brevicomis* than many other pine materials. He also first demonstrated that adult beetles carried microorganisms capable of fermenting an aqueous phloem extract. Struble[3] isolated these microorganisms from the intestinal tract and integument of larvae and adults and identified them as yeasts. In 1930 Person inoculated phloem strips with this isolated but unidentified yeast. This yeast-inoculated phloem attracted adult beetles during the first few (3 or 4) days after inoculation. This work provided the basis for the statements published by Person (1931).

In 1933 Gordon[4] studied the chemotropic responses of *Dendroctonus brevicomis* in an olfactometer. He tested a wide variety of chemicals and natural pine materials. The most positive attraction he observed was to phloem which had been standing in water exposed to airborne microorganisms. The attractivity of the inoculated phloem increased during the first 7 days in culture. After that time the attractivity declined until after 20 days the culture repelled the beetles. This repellent stage accompanied the production of acetic acid in the culture. Acetic acid production generally results from contamination with bacteria. Dethier (1947) reports a comparable finding, which showed that fermentation products were more attractive to a codling moth before alcohols and acids were formed. When acetic acid was formed, the bait actually repelled the moths.

Ten years later Struble[5] was not able to duplicate Gordon's results. He experimented with *Dendroctonus monticolae*. Many factors could contribute to such a disparity in results. Perhaps most important was the dependence of both workers upon the inoculation of the phloem with airborne microorganisms. Such random inoculations might not produce the same attrahent or in the same amount as would inoculations of bark-beetle yeasts.

Most recently Lu *et al.* (1957) demonstrated the attractivity to *Dendroctonus pseudotsugae* of dextrose-malt cultures of *Saccharomyces pastoria* (sic). This yeast probably is synonymous with *Pichia pastori* (Guilliermond) Phaff (1956). Their olfactometer was modified from one constructed 25 years ago by Gordon. They did not test the attractivity of yeast-inoculated phloem.

Working with *Drosophila*, several scientists have shown that yeasts—through differences in their metabolism—produce dif-

[2]N. T. Mirov. A preliminary study of attraction with the western pine beetle, *Dendoctonus brevicomis* Lec. Bureau of Ent. and Plant Quar., 1928. Typewritten report on file at Pacif. Southw. Forest and Range Expt. Sta.

[3]G. R. Struble. Memorandum of nutritional studies of western pine beetle larvae. Bur. Ent. and Plant Quar., 1930. Typewritten report on file at Pacif. Southw. Forest and Range Expt. Sta.

[4]A. Gordon. Apparatus used in a study of the western pine beetle. Bur. Ent. and Plant Quar., 1933. Typewritten report on file at Pacif. Southw. Forest and Range Exp. Sta.

[5]G. R. Struble. Preliminary results of the olfactory responses of the mountain pine beetle —season of 1943. Bur. Ent. and Plant Quar., 1944. Typewritten report, Pacif. Southw. Forest and Range Expt. Sta.

ferent attrahents for *Drosophila* species (see Shihata and Mrak, 1952, for further references). Refined work with *Dendroctonus* species and their yeasts might show a parallel relationship.

Yeast Floras of California Bark Beetles

A renewed interest in this positive attraction arose from the studies of the bark-beetle resistance of pines. A necessary step, then, was to identify the yeasts to be used in attraction studies. Shifrine and Phaff (1956) isolated 160 yeast cultures from intestinal smears and identified them as belonging to 13 species (Table 1). Five of these were new species, and one, *Saccharomyces pini* (Holst), subsequently was renamed *Pichia pini* by Phaff (1956). Usually they found only one type of yeast on each plate; occasionally two yeasts were isolated, and rarely three were present. More than three different yeasts never were found on one plate. This corresponds to reports by Grosmann (1930) and Lu *et al.* (1957).

One question to answer was: What was the distribution of specific yeasts on the different hosts of the bark beetles? A compilation and extension of Tables 1 and 3 from Shifrine and Phaff shows this distribution (Table 1). Four yeasts were found quite frequently. One might speculate on their distribution on the species of pines. Absolute numbers may mean very little, but the absence of species may be quite significant. Neither *Pichia pini* nor *Candida curvata* (Diddens et Lod.) Lodder et van Rij was found on *Pinus jeffreyi* (Grev. and Balf.). *C. curvata* also was not found on *P. monticola*. Further work must be done before definite host lists can be compiled for these yeasts. Yet the present information justifies the presentation of a working hypothesis: these two yeasts may not be able to utilize tissues of *P. jeffreyi* as a substrate for development.

Why should *Pinus jeffreyi* be unsuitable? For one thing, it is strikingly different from other pines in composition of its essential oils (Mirov, 1948). These oils are present in the tissues infected by the yeasts. Mossel (1951) has evidence that the terpenes from the essential oil of orange in-

TABLE 1. Number of cultures of each yeast isolated from Ips *and* Dendroctonus *beetles infesting various pines.*

Yeast	Tree species infested[1]				Total
	Pp	Pj	Pm	Pc	
Pichia pini (Holst) Phaff 1956	23	0	8	1	32
Hansenula capsulata Wickerham 1951	19	7	7	3	36
Candida silvicola Shif. & Phaff 1956	14	29	11	15	[2]70
C. curvata (Diddens et Lod.) Lodder et van Rij 1942	13	0	0	2	15
C. parapsilosis (Ashf.) Langeron et Talice 1928	2	--	--	--	2
C. mycoderma (Reess) Lodder et van Rij 1952	1	--	2	--	3
C. rugosa (Anderson) Diddens et Lodder 1917	--	1	--	--	1
Torulopsis nitratophila Shif. & Phaff 1956	1	--	--	--	1
T. melibiosum Shif. & Phaff 1956	2	--	--	--	2
Rhodotorula crocea Shif. & Phaff 1956	--	1	--	--	1
Cryptococcus diffluens (Zach) Lodder et van Rij 1934	2	--	--	--	2
Cr. neoformans (Sanfelice) Vuillemin 1894	1	--	--	--	1
Pichia haplophila Shif. & Phaff 1956	--	3	--	--	3
					169

[1] *Pinus ponderosa* (Pp), *P. jeffreyi* (Pj), *P. monticola* (Pm), and *P. contorta* var. *latifolia* (Pc).

[2] A single culture of this yeast was obtained from an *Ips confusus* Lec. adult taken from *Pinus lambertiana* Lamb.

TABLE 2. The species of yeast associated with Dendroctonus *and* Ips *bark beetles infesting different pines.*

Insect species	Pine species	Yeast species (number of cultures)
D. brevicomis	*ponderosa*	*P. pini* (18), *C. parapsilosis* (2), *Cr. diffluens* (1), *Cr. neoformans* (1)
D. jeffreyi	*jeffreyi*	*H. capsulata* (6), *P. haplophila* (2), *C. silvicola* (4), *C. rugosa* (1), *R. crocea* (1)
D. monticola	*ponderosa*	*H. capsulata* (17), *P. pini* (3), *C. silvicola* (8), *C. curvata* (8), *T. nitratophila* (1) *T. melibiosum* (2), *Cr. diffluens* (1)
	monticola	*H. capsulata* (7), *P. pini* (6) *C. silvicola* (10), *C. mycoderma* (1),
	contorta v. *latifolia*	*H. capsulata* (3), *C. silvicola* (4), *C. curvata* (1).
D. valens	*ponderosa*	*C. silvicola* (1)
	jeffreyi	*C. silvicola* (1)
I. oregoni	*ponderosa*	*H. capsulata* (1), *C. silvicola* (4), *C. mycoderma* (1)
	jeffreyi	*H. capsulata* (1), *C. silvicola* (18)
	contorta v. *latifolia*	*P. pini* (1), *C. silvicola* (11), *C. curvata* (1)
I. confusus	*ponderosa*	*H. capsulata* (1), *P. pini* (2), *C. silvicola* (1), *C. curpata* (5)
	monticola	*P. pini* (2), *C. silvicola* (1), *C. mycoderma* (1)
	lambertiana	*C. silvicola* (1)
I. emarginatus	*jeffreyi*	*P. haplophila* (1), *C. silvicola* (6)

hibit the fermentation activity of the yeast *Saccharomyces cerevisioe*. Perhaps the two yeasts not found in *P. jeffreyi* have not evolved a tolerance for the unique turpentine constituents found in this pine.

Another question was: Were particular yeasts associated with each species of bark beetle? A new summary of the yeasts that Shifrine and Phaff found with the various species of bark beetles is given in Table 2. Several species of yeast were found to be associated with each species of bark beetle where many individuals had been examined. No species of bark beetle was exclusively associated with any one yeast, and no yeast was specifically associated with a single bark beetle species. However, the data suggest that *Hansenula capsulata* Wick. and *Pichia pini* were more frequently associated with *Dendroctonus* species. Particularly *D. brevicomis* had *P. pini* as its most frequent associate. Of course such conclusions may not be extended to those yeasts encountered only infrequently. Seasonal fluctuation in the composition of these flora was not followed as it has been in *Drosophila* (Shihata and Mrak, 1952).

It is also significant that the isolated yeasts were internally associated with every species of bark beetle. Yeasts were found through all stages of beetle metamorphosis from the smallest larvae to the adult beetles flying to the next host tree. They were present in the non-feeding pupal and callow adult stages as well as in the feeding larval and adult stages. Eggs were not cultured, but Grosmann (1930), Leach *et al.* (1934), and Holst (1937) indicated that the eggs too are contaminated, at least externally.

Of the specimens representing each stage of metamorphosis, between 80 and 90 percent yielded yeast cultures. The remaining 10 to 20 percent of the specimens either were devoid of yeast or no longer contained viable yeasts. The latter possibility was substantiated by the observation of non-viable yeast cells in the guts of some of these specimens from which yeast cultures were not obtained. During the course of this work

the digestion of the intestinal flora was noted. Complete digestion occurs within a few days, especially at higher temperature. An analogous situation was found in *Drosophila* by Shihata and Mrak (1951, 1952) and in a dried fruit beetle by Miller and Mrak (1953).

The Thermal Relationships of the Yeasts

Shifrine (1954) studied the ability of the yeasts, isolated from bark beetles, to grow at various temperatures. Six temperatures of incubation were used: 0°, 5°, 13°, 31°, 34°, and 39°C. The medium used for the test consisted of 1 percent glucose plus 0.5 percent yeast extract in distilled water. The medium was sterilized in 16 mm tubes and then inoculated from young wort agar slant cultures. The results after two weeks of growth (Table 3) were read by the method of Wickerham (1951).

The thermal responses of most of the yeasts corresponded closely to the thermal responses of at least one bark-beetle species. Miller (1931) found that the larvae and adults of *D. brevicomis* were active from 7° to 35°C. This temperature range corresponds closely to the range of temperature in which most bark-beetle yeasts showed moderate to good growth. At 39°C, the yeasts did not grow well; this temperature corresponds closely to the temperature at which Miller found that larvae became sluggish and finally paralyzed. Probably at 5°C and certainly at 0°C, Miller found that all brood stages became dormant; at these low temperatures the growth of the yeasts also slowed considerably. Certain yeast cultures, however, did grow at 0°C and most grew at 5°C.

Both Holst[6] and Rumbold (1941) have reported that 27°–30°C are the optimum temperatures for the growth of bark-beetle yeasts. Shifrine's data coincide with this earlier work. Holst reported growth of his yeast (*Pichia pini*) was very slow at 4°C, while most of Shifrine's yeasts grew well at 5°C. Good growth at such low temperatures is not common for most yeasts. Hence, this finding may contribute to our understanding of the ecology of the yeasts and the bark beetles with which they associate.

Conclusions

This summary of studies of the association of yeasts and bark beetles impresses one with the fragmentary nature of knowledge.

[6]E. C. Holst. Report on the yeast-like organisms associated with the blue stain of wood. Bur. Ent. and Plant Quar., 1931. Typewritten manuscript on file at Pacif. Southw. Forest and Range Experiment Station.

TABLE 3. Number of yeast cultures exhibiting poor to no growth (—) or moderate to good growth (+) after incubation for two weeks.

	Incubation temperature											
	0°C.		5°C.		13°C.		31°C.		34°C.		39°C.	
Yeast species	+	—	+	—	+	—	+	—	+	—	+	—
Pichia pini	0	12	11	1	12	0	12	0	4	8	0	12
Hansenula capsulata	2	15	16	1	17	0	17	0	16	1	1	16
Candida silvicola	6	29	35	0	35	0	35	0	30	5	5	30
C. curvata	8	6	14	0	14	0	14	0	14	0	7	7
C. mycoderma	0	3	0	3	0	3	3	0	3	0	0	3
C. rugosa	0	1	1	0	1	0	1	0	0	1	0	1
Torulopsis melibiosum	0	2	0	2	2	0	2	0	0	2	0	2
Cryptococcus diffluens	0	1	1	0	1	0	1	0	0	1	0	1
Pichia haplophila	0	3	0	3	3	0	3	0	0	3	0	3

Source: Shifrine (1954).

The work of Grosmann and that of Shifrine and Phaff indicate that an individual insect specimen usually has only one associated yeast, although infrequently specimens may have two or rarely three yeast associates. The latter authors have demonstrated that the bark-beetle and pine species studied do not have specific associated yeasts. Each individual insect, then, generally has only one yeast, but the individuals of a species, be they bark beetles or trees, vary in their yeast associates. The yeast floras of many species of bark beetles should be analyzed; studies should be made of geographic and seasonal variations in yeast floras of the bark beetles which have already been investigated.

Little is known about the composition of these yeast floras, even less about the nature of the interaction between bark beetles and yeasts. We have only fragmentary knowledge of the general consociation of the two organisms: the development of yeasts inoculated into the phloem, the attraction of bark beetles to yeast-fermented phloem, and the ingestion and subsequent digestion of yeasts by all feeding stages in the bark beetle life cycle. Little is known but much is supposed about the role of yeasts in bark-beetle attraction. Actually, Person was the only worker to demonstrate a positive attraction of a bark beetle to a phloem ferment produced by yeasts isolated from that bark beetle. The attraction was weak and only lasted a few days, after which a repulsion set in. Well-designed studies could clarify the role of yeasts in the production of bark beetle attrahents and in the nutrition of bark beetles.

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Poplars and Eucalypts

Pubblicazioni del Centro di Sperimentazione Agricola e Forestale. Ente Nazionale per la Celulosa e per la Carta. (Publications of the agricultural and forest experiment station. National organization for pulp and paper). 1:1-249, 1957; 2:1-266, 1959. Rome.

Review by John W. Duffield
Industrial Forestry Association
Nisqually, Washington

Attention is called to a new series of publications dealing with poplars and eucalypts grown in Italy for the production of pulpwood. These papers, covering the fields of morphology, anatomy, soils, entomology, pathology, zoology, mensuration, logging, wood technology, and silviculture, are the work of the staff of the Agricultural and Forest Experiment Station of the National Organization for Pulp and Paper in Rome, under the direction of Prof. A. de Philippis of the University of Florence.

Volume I, published in 1957 assembles papers dealing with eucalypts presented to the First World Congress on Eucalypts in Rome in 1956. It consists of 14 papers, covering, in addition to the topics listed above, the Italian literature on eucalypts. Volume II contains 16 papers published as abstracts in 1958 and 1959. All papers have adequate English summaries as well as bilingual captions and explanatory notes for figures and tables. Although many of the papers deal with Mediterranean conditions, a substantial proportion of them, dealing with basic morphology, reproductive biology and wood technology are of more than regional interest.

These volumes set high standards in preparation, illustration, typography, and, of course, paper. They will be of great interest and value to foresters concerned with the cultivation and utilization of poplars, aspens and eucalypts.

Estimation of Certain Wood Properties of Loblolly and Slash Pine Trees from Breast Height Sampling

BY
BRUCE ZOBEL
FAYE HENSON
CHARLES WEBB

IT IS WIDELY RECOGNIZED that wood properties in a tree vary from the pith outward and from the base to the top of the tree. Such variation makes sampling of wood from individual trees very difficult, especially if samples are desired from a large number of trees.

In order to avoid taking wood samples at several points up the tree for estimating the characteristics of the total merchantable bole, considerable thought has been given to securing the total estimate by sampling at only one position in the tree. Perhaps the easiest position to work from is B.H. (breast height, i.e., 4.5 feet above average ground level). This measurement is a standard one in forestry. Most important, it is high enough up the bole to avoid the very large variations in wood properties often found at the base of the tree in the southern pines.

The value of being able to estimate the properties of a whole tree from a single, easily-reached sample is obvious. In fact, it is vitally important to researchers and foresters working in genetic or wood variation studies, where a large number of trees must be sampled rapidly without destroying them. Up to the present time, studies of genetic variation have been made, and breeding projects have been set up with the assumption that the specific properties under study at breast height would be closely related to those for the total bole. Such an assumption actually has involved a sizeable gamble; yet much research has been undertaken with the evident hope that the assumption is free of error.

Available literature contains few references to breast height-bole relationships. Mitchell (1958), Mitchell and Wheeler (1959a, 1959b) and Wahlgren and Fassnacht (1959) recently reported that the correlation coefficients for specific gravity between breast height and total tree bole for loblolly pine and for slash pine were 0.7291 and 0.4991, respectively. Researchers in Australia found for hoop pine (*Araucaria cunninghamii*) (Anonymous 1957) that specific gravity values at breast height were correlated with total tree values. Miller (1959) reported a correlation coefficient of about 0.86 for slash pine when comparing the specific gravity of the midpoint of the first pulpwood bolt with the weighted average specific gravity of the merchantable portion of the tree.

While working out a quick and simple sampling method to determine the fiber dimensions of potential pulpwood species in

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the Malayan forests, Peel (1958) found that fiber characteristics obtained from chips taken at waist height showed remarkable similarity to fiber characteristics for the whole tree. This was particularly true in samples from mature trees. No publication was found that dealt with such a relationship for cellulose yields; however, P. Schutt (Schmalenbeck, Germany)[1] states that work is being done on the variations of the cellulose content in relation to stem height and diameter. In a recent paper, Zobel *et al.* (1959) reported certain relationships found between core wood (B.H.) and total core wood; also between core wood (B.H.) and total wood in the bole.

In the present paper, results of the investigations on specific gravity and cellulose yields of loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm. var *elliottii*) are reported. These results represent confirmatory information for specific gravity for two pine species and the first published information (to the authors' knowledge) on relationships of cellulose yields at B.H. to cellulose yields of the total tree bole.

Research Method

General. In order to determine dependable relationships between breast height and total tree values for specific gravity and cellulose yields, several trees had to be sampled, with a number of samples from each tree. To determine the specific gravity relationships, 45 slash pines from the Sandhills of South Carolina, averaging 17 years old, were studied along with 14 loblolly pines from the Coastal Plain of North Carolina.[2] Three of the loblolly pines were 50 years old and 11 were 17 years old. Of these trees, 16 slash pines and 10 loblolly pines (three 50 years old and seven 17) were used in the cellulose studies. Specific gravity and cellulose yields were determined from the same wood sample.

The slash pines were sectioned every five feet and the loblolly pines every two feet. One-inch thick cross-section disks were cut at each sampling location; from these, a strip approximately one inch wide was cut through the center of the disk. These strips were then divided by a rough visual method (Zobel, *et al*, 1959) into core[3] and outer wood, and determinations were made of their specific gravity and cellulose yields. Averages for each disk and for each tree were obtained by weighting the core and outer wood values by the areas and volumes, respectively, which they occupied.

Methods used to determine specific gravity and cellulose were those described previously by Zobel and McElwee (1958a, 1958b), and Zobel *et al.* (1959). In brief, specific gravity was obtained by the standard relationship of dry weight to green volume. Two types of cellulose were obtained by a "micro" procedure in which a number of determinations were made concurrently. One type of cellulose, termed water-resistant carbohydrates (WRC), was obtained by a chloriting treatment producing a product somewhat similar to holocellulose. The alpha-cellulose was obtained by treatment with sodium hydroxide.

Relationships determined. Several different relationships relative to breast height and total tree values were determined. The solid black areas shown in Figure 1 were correlated with the cross-hatched areas. Relationships were determined for total B.H. values to total tree volume (Fig 1, No. 1); this includes outer plus core wood values at B.H. compared to outer plus core

[1]Personal communication, 1959.

[2]Slash pines collected and furnished by Southeastern For. Expt. Sta., U.S. Forest Service, as samples in a study of volume-weight relationships, and loblolly pines used by Haught (1958) in his study of compression wood.

[3]Near the pith of the bole there is a cylinder of relatively low specific gravity, low cellulose-yielding and short-fibered wood, changing rapidly from the pith outward. It extends through the length of the bole and its diameter appears to remain fairly constant within a tree, but varies between trees. The wood outside this core, called outer or mature wood, has higher specific gravity, higher cellulose yields and longer fibers.

wood of the total merchantable bole. Values thus obtained are comparable to those reported in papers such as the one by Mitchell and Wheeler (1959a). Relationships were determined for outer B.H. (exclusive of all core wood) to total outer wood of the bole, which in older trees constitutes the bulk of tree volume (No. 2), as well as outer B.H. to total tree volume (No. 3). Similar determinations were made involving core wood (Nos. 4 and 5). Some previously reported relationships obtained for core wood (Zobel *et al.* 1959) appear again in Table 1.

Results

Specific gravity relationships. The relationships of specific gravity values between breast height and the entire bole, as shown by both the regression analyses and the correlation coefficients, are strong (Table 1). Initial plotting indicated a linear relationship; thus, use of a simple regression coefficient is adequate. The strongest relationships are those where total cross section at B.H. is compared with the entire bole (No. 1) or when outer wood at B.H. is compared to the outer wood of the entire bole (No. 2); they are especially strong for slash pine where about 40 trees were sampled. However, even for loblolly pine, which involved only about 14 trees, (3 of which were 50 years of age, compared to 17 years for the other 11) the significance of the relationship is also very clear.

Special attention should be directed to the relationship of core values at B.H. to total bole (No. 5, Table 1). Although this is not the strongest correlation found, it is highly significant, and sufficiently so to suggest the possibility of predicting the specific gravity of the whole mature tree from a knowledge of the specific gravity of the wood of a young tree.

No regression equations are reported in this paper, since the objective was simply to demonstrate the strength and magnitude of the several associations. With these relationships established, collection of data seems warranted in any specific area where it is desired to develop regression equations as a predictive mechanism. Regression coefficients are shown here to indicate the magnitude of change in bole values with a unit change in breast height values. Note that this change is generally more rapid for slash pine than for loblolly pine. The small size of the standard errors of estimates is gratifying.

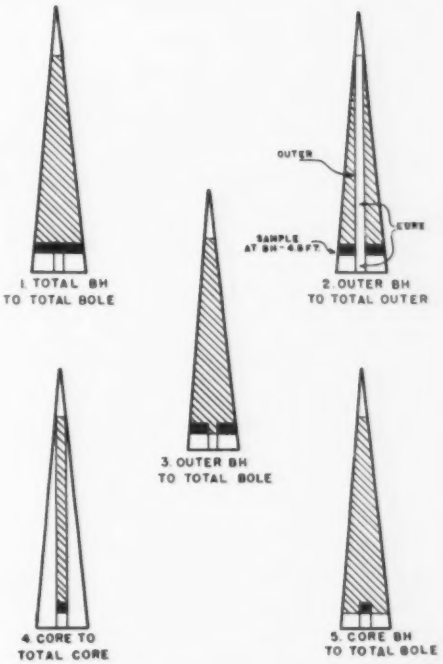

FIGURE 1. *Graphic representations of the relationships determined. The black area shows the breast height sample which is correlated with the crosshatched portion. (See text for explanations.)*

As an example of the character and strength of the relationships, Figures 2 and 3 were plotted to represent the first two lines (1) and (2) in Table 1 for slash pine.

Cellulose yield relationships. Cellulose yields show much the same pattern as specific gravity for both slash and loblolly pines (Table 2). The cellulose analyses were

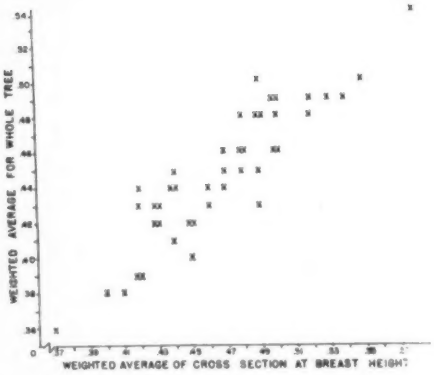

FIGURE 2. *Plotted relationships between breast height values of specific gravity for the whole cross section and for the total bole in slash pine. This is No. 1 in Figure 1.*

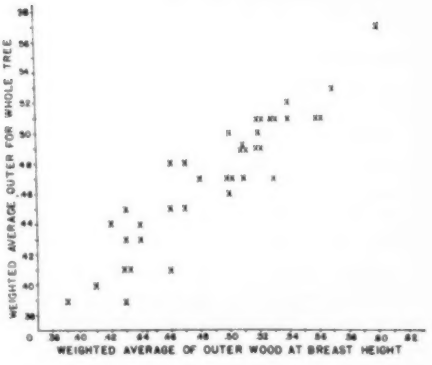

FIGURE 3. *Plotted relationships between breast height outer wood values of specific gravity and outer wood for the whole bole in slash pine. This is No. 2 in Figure 1.*

TABLE 1. Relationship of specific gravity at breast height[1] to specific gravity of the total tree bole.

Relationship[2]	Number of trees sampled	Regression coefficient (b)	Standard error of estimate	F	Correlation coefficient
		SLASH PINE			
Total B.H. to total bole (1)	43	.801	.016	185.41**	.905**
Outer B.H. to total outer (2)	38	.806	.016	237.93**	.931**
Outer B.H. to total bole (3)	42	.696	.016	173.67**	.902**
Core B.H. to total core (4)	45	.773	.015	156.90**	.886**
Core B.H. to total bole (5)	40	.500	.025	66.05**	.798**
		LOBLOLLY PINE			
Total B.H. to total bole (1)	14	.673	.013	45.58**	.892**
Outer B.H. to total outer (2)	14	.676	.011	39.23**	.876**
Outer B.H. to total bole (3)	14	.405	..	3.01 N.S.	.446 N.S.
Core B.H. to total core (4)	14	.574	.022	17.50**	.770**
Core B.H. to total bole (5)	13	.681	.013	42.78**	.890**

[1]4.5 feet above general ground level.
[2]Numbers in parentheses refer to diagram numbers in Figure 1.
**Significant at 1 percent level; *significant at 5 percent level; N.S. = Non-significant.

TABLE 2. Relationship of cellulose yields at breast height[1] to cellulose yields of the total tree bole.

Relationship[2]	Type of cellulose	Regression coefficient (b)	Standard error of estimate	F	Correlation coefficient
		A. SIXTEEN SLASH PINE TREES			
Total B.H. to	WRC	1.064	.44	60.45**	.901**
total bole (1)	Alpha	.765	.95	25.16**	.800**
Outer B.H. to	WRC	.737	.40	42.69**	.861**
total outer (2)	Alpha	.907	.81	57.65**	.897**
Outer B.H. to	WRC	.659	.59	15.12**	.721**
total bole (3)	Alpha	.744	1.00	25.22**	.802**
Core B.H. to	WRC	.655	.69	94.98**	.934**
total core (4)	Alpha	.847	.92	60.83**	.902**
Core B.H. to	WRC	.206	.65	10.75**	.659**
total bole (5)	Alpha	.341		3.82 N.S.	.463 N.S.
		B. NINE LOBLOLLY PINE TREES[3]			
Total B.H. to	WRC	.970	.68	6.60*	.697*
total bole (1)	Alpha	1.207	.57	50.70**	.938**
Outer B.H. to	WRC	.620	.45	14.80**	.824**
total outer (2)	Alpha	.555	.46	22.14**	.872**
Outer B.H. to	WRC	.575	.32	24.85**	.883**
total bole (3)	Alpha	.564	..	4.95 N.S.	.644*
Core B.H. to	WRC	.908	.93	60.40**	.947**
total core (4)	Alpha	.774	.70	25.52**	.886**
Core B.H. to	WRC	.193	.36	17.67**	.846**
total bole (5)	Alpha	.150	..	0.30 N.S.	.202 N.S.
		C. TEN LOBLOLLY PINE TREES[3]			
Total B.H. to	WRC	.667		4.25 N.S.	.589 N.S.
total bole (1)	Alpha	.969	.79	22.32**	.858**
Outer B.H. to	WRC	.611	.42	18.44**	.835**
total outer (2)	Alpha	.410	.67	6.63*	.673*
Outer B.H. to	WRC	.367	..	2.50 N.S.	.487 N.S.
total bole (3)	Alpha	.310	..	1.01 N.S.	.336 N.S.
Core B.H. to	WRC	.890	1.07	44.11**	.920**
total core (4)	Alpha	.779	.66	44.51**	.921**
Core B.H. to	WRC	.178	.41	5.48*	.638*
total bole (5)	Alpha	−.94	..	0.15 N.S.	.135 N.S.

[1]4.5 feet above general ground level.
[2]Numbers in parentheses refer to diagram numbers in Figure 1.
[3]See text for explanation.

**Significant at 1 percent level.
*Significant at 5 percent level.
N.S. = Non-significant.

made for both WRC[4] and alpha-cellulose according to the method developed by Yundt and Bradway and described by Zobel and McElwee (1958).

The portion of the table dealing with

[4]Water-resistant carbohydrates (similar to holocellulose).

loblolly pine needs special explanation. As shown, values are given for nine trees and also for ten trees. As can be seen, the correlation coefficients and regression coefficients are higher when nine trees were used than when ten were used.

Upon plotting the ten-tree data for alpha-cellulose and WRC, it was immediately noted that nine of the trees showed a close pattern, but one of the trees was much outside the pattern for WRC, and a different tree was outside for alpha-cellulose (Fig. 4). An intensive check of the data disclosed no calculation error, though a re-check of the cellulose yields was not possible due to the destruction of the sample in making the original analysis.

Therefore, the authors decided to report two sets of results, with nine and ten trees, and let the reader draw his own conclusions. An error in measuring the B.H. sample of the "errant" trees could cause the difference; however, insofar as it was possible to check, no error could be found, so there seemed no justification for rejecting the tree. On the other hand, the authors feel that it would be just as incorrect to state that no relationship exists, when it is obvious from the plotted data (Fig. 4) that nine of the loblolly trees show a close relationship similar to that found for the slash pines.

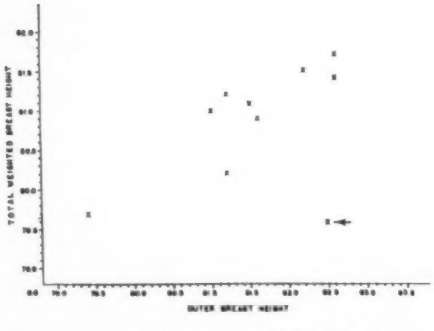

FIGURE 4. *Relationship of WRC (water-resistant carbohydrates, similar to hollocellulose) values at breast height to those for the whole tree bole. Note that nine of the trees fall in line; one is much out of line. (See text for discussion.)*

The relationships between B.H. and total tree values appear to be considerably closer for WRC than for alpha-cellulose. Especially where core wood is involved, alpha-cellulose relations seem to be erratic. However, it is most encouraging to see the very satisfactory results for the 16 young slash pines. The nine (or ten) loblolly pines, with mixed ages of 50 and 17 years, give somewhat poorer relationships. Especially noticeable are the considerably larger standard error of estimates for alpha-cellulose.

From the data presented here on the 16 slash and 10 loblolly pines, it appears that the WRC relationship of core to entire bole is acceptable. The standard errors of estimate are also quite satisfactory, considering the lack of refinement of the method of cellulose analysis. Dependence on this relationship for alpha-cellulose must be considered risky until more trees are sampled or a more refined method of alpha-cellulose analysis is used.

General relationships. The value of the relationship (Fig. 1, No. 1) of total B.H. to total tree bole is obvious for both specific gravity and cellulose yields. Nevertheless, use of this relationship has one big drawback; in certain areas, and especially for older stands, the core wood often contains an excessive amount of pitch and compression wood, which make accurate analyses of specific gravity or cellulose yields to the heart of the tree difficult. In such instances, it is fortunately feasible to use the relationship of outer wood at B.H. to total outer wood in the whole tree (Fig. 1, No. 2). The outer wood represents the bulk of the volume of the wood of older trees. As an estimate of the wood properties in the whole tree, the relationship of outer B.H. to total volume (Fig. 1, No. 3) is a most useful value. However, this is usually less well defined than B.H. outer to total outer, probably because of the pitch and other "extractives" commonly associated with the core wood.

For predictive purposes, especially for specific gravity in young trees, the relationships shown in Figure 1, Nos. 4 and 5, are valuable. The possibility of using a core wood sample from a young tree in predicting wood properties of the total tree values at maturity obviously enables shortening the time interval for undertaking progeny tests of wood characteristics of selected genetic material.

Relationships were determined by calculating the regression coefficients, as well as the correlation coefficients (Snedecor 1948). As indicated by Zobel *et al.* (1959), a recognized source of weakness is present in the calculations. The method used introduces various amounts of automaticity; i.e., the B.H. value used for predictive purposes is also a portion of the value used to characterize the total tree bole. Brandt (1941) and others have appropriately cautioned that such a correlation must automatically be different from zero. Since the portion contributed by the B.H. sample is normally small, failure to start with a zero hypothesis is not too serious.

Discussion and Summary

It would appear from the data presented here, and from other published results, that it is satisfactory to use breast-height characteristics of specific gravity and cellulose yields to indicate the characteristics of the entire tree. Thus, it is possible to get a good estimation of these wood characters for the whole tree simply by obtaining a sample at B.H. Studies of tree-to-tree variability and of inheritance of wood characteristics, as well as routine determination of wood specific gravity and cellulose yields, can be simply made by obtaining breast height specimens.

The closest relationships are obtained by comparing total B.H. values to those of the total tree hole. This procedure is highly satisfactory for young stands. However, for older trees which contain heartwood or pitch, or for trees that have defects or compression wood at the heart, the most practical measurement to use is outer wood at B.H. to total outer wood in the tree bole. In the intensive studies on genetics of wood at North Carolina State College, this measurement is the one that is employed. Feasibility of employing B.H. core values will be very useful for young stands or for predictive purposes, making possible assessment of potential wood properties of very young trees.

The previously reported relationships indicate, for example, that if specific gravity at B.H. is high, the average specific gravity for the whole tree bole will be high. For maximum use of this information, a method must be devised for translating B.H. values into average values for the whole tree. Such a method has been described by Mitchell and Wheeler (1959) and Wahlgren and Fassnacht (1959) whereby regression equations were determined, thus making it possible to find the average value for a given tree from a known B.H. value. Such a transformation is very valuable and enables the reporting of survey and cruise data, not only as cords of wood, but also as pounds of wood. If cellulose information is available, then inventories of growing timber can report, in addition to cords and pounds of wood, the pounds of cellulose present and being added yearly. Information of this nature will be highly useful in intensive forest management.

Not enough information is yet available to publish generalized regression equations for either specific gravity or cellulose yield. Yet, the reported data of Mitchell and Wheeler (1959) for specific gravity on the four southern pines in Mississippi show the curves to be quite similar. Until more is known, however, it is still necessary to sample enough trees in an area so that an equation applicable to that area can be determined.

The most encouraging point, illustrated by our data and the other reported papers, is that for specific gravity and certain cellulose yields a sample at breast height can be used as a satisfactory indicator of this characteristic for the whole tree. It appears that fiber length may follow the same pattern,

although as yet not enough data are available to determine their statistical significance.

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Female Flowers on One-Year-Old Pitch Pine

By Gene Namkoong,[1] *Forest Service, U. S. Department of Agriculture*

Precocious flowering of tree species is of particular interest to forest geneticists because of the opportunity it offers to produce F_1 and later generations, under control, in less time than is usually required of forest trees.

Righter,[2] reporting on early flowering of 56 species and varieties and one species hybrid, gave a minimum average of 4.4 years for male flowers and 5.2 years for female flowers. The earliest trees to produce male flowers were one-year-old *Pinus sinensis*, and the earliest for female flowers were two-year-old *P. densiflora*, *P. densiflora* var. *globosa*, and *P. sinensis*. Subsequently, male and female flowers were reported on two-year-old *P. rigida*,[3] female flowers on two-year-old *P. greggii*,[4] and male flowers on 11-month-old *P. mugo*.[5]

This note records what may be a new degree of precocity for pines—the production of female flowers in *Pinus rigida* at 12 months from seed. A total of four flowers were found in April 1959 on three out of twenty potted seedlings of an intraspecies *P. rigida* hybrid. The original source of the parent trees is near Atlantic City, New Jersey, and the cross was made at the Western Institute of Forest Genetics. The seeds were collected in 1955 and sown in the nursery near Gulfport, Mississippi, in April 1958. The resulting seedlings were potted in January 1959.

Such extreme precocity was not expected, and the flowers may have passed the pollen-receptive stage before they were discovered. They were, however, bagged and pollinated with slash pine pollen. Thus far, two conelets have aborted and the remaining two, on two seedlings, appear healthy. Figure 1 shows one of these.

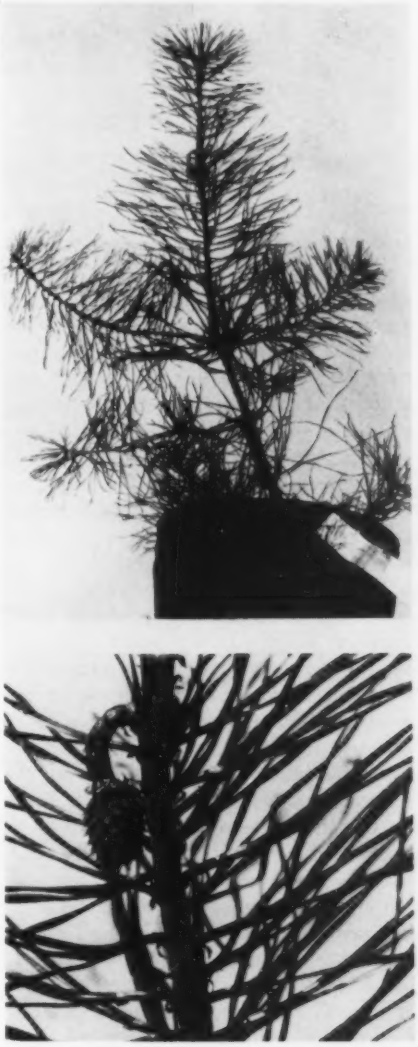

FIGURE 1. *Conelet on one-year-old pitch pine. These photographs were taken in June, two months after bud-break and flowering.*

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[1]Stationed at the Southern Institute of Forest Genetics, Gulfport, Miss., a unit of the Forest Service's Southern Forest Experiment Station.

[2]Righter, F. I. Early flower production among the pines. J. For. 37: 935-938. 1939.

[3]Andresen, J. W. Precocity of *Pinus rigida* Mill. Castanea 22: 130-134. 1957.

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Crown Length and Crown Ratio As Indicators of Diameter Growth of Loblolly Pine

BY
H. FAIRFIELD SMITH
DAVID A. DUBOW

THE RELATION of growth of trees to some dimensions of their crowns has been considered in many mensuration studies. In particular, the ratio live crown length/total height has frequently been used in the past under the assumption that it provides a simple index of growth vigor, or that it indicates the need for thinning.

Similar ratios have been used often by biologists because of a belief that they may be more stable in varying environments than are the primary characters. In plant breeding, for example, the grain/straw ratio has been taken as an indicator of the potentiality of cereals to produce grain. However, Smith (1936) pointed out that utilization of such ratios implies a subjective or theoretical and arbitrary guess at the modes of variation of each character under different influences; and that substantially more information may be gleaned from the primary characters with attention to what is in fact their observed mutual variation in prescribed circumstances.

In forestry detailed consideration has been given to a number of interrelationships of crown development and growth as exemplified by studies of Mar:Moller (1947), Holsoe (1948, 1951), Burger (1953), and others. However, and understandably, practical interests have been directed more toward single indexes of tree vigor and growth because of their seemingly greater facility in application; hence the frequent employment of such composites as crown/height ratio.

The purpose of this paper is to examine somewhat critically how crown and stem lengths are related to the vigor of loblolly pine (*Pinus taeda* L.) as reflected in periodic diameter growth. Such relationships may vary considerably according to circumstances. They may be differentially affected by genetic and environmental variation, both locally (between trees within a given site) and geographically (between sites of variable quality).

Since the present study covers only three small areas within a single locality, the results have limited applicability, but they may

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give useful hints for wider exploration as opportunities occur.

Experimental Material

The data are derived from three loblolly pine plantations of different ages in which fertilizer experiments were installed in the winter of 1950-1951 (Table 1). The plantations are situated within half a mile of each other within the Hill Demonstration Forest, Durham County, North Carolina. Detailed description of their soil, vegetation and treatment history is given by Brenneman (1953). Plots consisted of areas in which 80 trees were initially planted. Within the plots the central 2 rows were observed, the remaining rows serving as isolation. The numbers of trees surviving and measured in the test areas ranged from 6 to 14, 11 to 20 and 12 to 18 per plot, in plantations A, B, and C, respectively. Experimental fertilizers were applied in March, 1951, 1952, and 1953, the treatments being various combinations of nitrogen, phosphate and potash. An analysis of the effects of fertilizer three growing seasons after the first application indicated that nitrogen was the only element producing detectable response.

Regressions of Diameter Growth on Crown and Stem Lengths

Graphs of diameter growth (for individual trees from several plots) against crown length, and against crown length/total height ratio, indicated that no significant curvature of regressions could be detected. Therefore only linear regressions have been computed. For all regressions here considered, the dependent variate is the diameter increment in inches d.b.h., for three growing seasons (1951 to 1953 inclusive); ie.

y = 3-year diameter increment (inches d.b.h.) for the growing seasons 1951-1953.

The following notation is used for the independent variates:

c = live crown length (feet) in 1953

s = stem length = height from ground to base of live crown (feet) in 1953

h = total height = $c + s$

r = live crown length:total height ratio = c/h.

Since in statistical computations it is generally undesirable to have one observation include another, we prefer to deal with stem length (s) rather than with total height (h). It is easy to transfer the final statistics from one to the other. To save computation on obtaining regressions on r and related statistics we used an approximate linear transformation from c and s to r, namely, the linear terms of a Taylor expansion for deviations about the means of each variate, $(r - \bar{r}) \doteq [\bar{s}\,(c - \bar{c}) - \bar{c}\,(s - \bar{s})]/\bar{h}^2$, where $\bar{r}$ = the mean of r, etc. To check validity of the approximation, statistics for actual ratio per tree were evaluated for plantation B with results as follows:

	Regr. coeff. y on r	*Variance about regr.*	*Squared correl. coeff.*
Using true r per tree	.0374	.0820	.378
Using approximation	.0391	.0784	.405

The approximate procedure errs on the side

TABLE 1. Characteristics of three loblolly pine plantations (1953 averages).

Plantations	Total area	No. of plots	Age of plantation in 1953	Spacing	Height	Crown length	Crown length/ total height ratio	D.B.H.	No of trees observed
	Acres		*Years*	*Feet*	*Feet*	*Feet*	*Percent*	*Inches*	
A	2	26	19	6 x 6	44.7	16.7	37.4	6.1	251
B	2	26	15	6 x 6	35.9	13.2	36.7	4.6	393
C	1¼	22	13	6 x 4	32.9	12.5	38.1	4.3	320

of showing too high a correlation. It is thus conservative with respect to conclusions drawn in this paper: to use true values of r would make our conclusions a shade more emphatic.

The data from plantation A were intensively analyzed to study variation of the regressions with the different classifications into which total variation could be partitioned, namely between trees within plots, between plots within nitrogen levels and between nitrogen levels. The details of the resulting rather complex analysis of variance will not be presented here. Suffice it to say that overall regressions and partial regression coefficients of diameter growth on tree number per plot, live crown length and stem length were each very highly significant. The regression on tree number, which can only be determined between plots, was not affected by nitrogen level. The regressions on crown length and stem length showed significant interaction with nitrogen level (at the 5 percent and 2 percent significance levels respectively), but the variation was small relative to the magnitude of the average regression.

Apart from variation of slopes, the regressions are at slightly different levels for each nitrogen level. This means that a regression which may be useful to predict relative growth rates between trees subject to natural variation is not adequate to predict absolute growth rates under different fertilizers. The result could be anticipated since we are considering growth *increments* contemporaneous with the application of fertilizer. Total diameter might be fully reflected in crown and stem lengths, or diameter increment might be fully reflected in crown and stem increments; but we could not expect crown and stem lengths, most of which were determined before fertilizers were applied, to show fully the immediate boost to contemporary growth.

Regressions on crown and stem lengths were not significantly different between and within plots, that is, were not detectably affected by variation of stand and of plot to plot fertilities. Table 2 presents the within-plot regressions as they are slightly more accurately determined than are those for overall variation.[1] Crown and stem lengths are practically uncorrelated, hence partial regression coefficients are almost the same as the zero order regressions on each variable without attention to the other.

As an index to which characters may be the best predictors for another, most writers in the past have considered the correlation coefficient. This can, however, be a treacherous index because of its susceptibility to range of variation explored. In general a safer measure of the quality of a prediction equation is the variance of the dependent variate about the regression. However, when, as here, one has to deal with naturally occurring variation it may happen that, over different plantations, variance about the regression stays roughly proportional to total variance. Since that proportion is the complement of the square of the correlation coefficient, the correlation would in such circumstances be a suitable index. Preferred choice depends on whether absolute or relative variances about regressions remain more stable. Since growths in the three sites observed have almost equal total variances they give no evidence for the preferred choice in this work. Therefore, for possible convenience of comparisons to future work, Table 2 presents both the variances about regressions and the squares of the correlation coefficients.

Correlation of diameter growth with live crown length seems to be increasing with age, that with stem length to be decreasing, but these changes are not statistically signifi-

[1]The effects of including between-plot variation are: (1) negligible on regressions on live crown length (c); (2) to decrease regressions on "clear" stem length (s) and hence also on total height (h); (3) negligible on regressions on live crown length:total height (r); (4) to increase all variances (as would be expected); (5) to decrease squared correlations with c and s by about .02, with h by about .12; (6) correlation with r is almost unaffected (and still remains substantially lower than the correlation with c).

TABLE 2. Comparison of average within-plot regressions of diameter growth (in inches) on crown length (in feet) and its compounds with height.

	Plantation					
	A (19 yrs. old)		B (15 yrs. old)		C (13 yrs. old)	
Regression coefficients						
On live crown length (c): partial reg.	.0620		.0852		.0849	
On clear stem length (s): partial reg.	.0297		.0247		.0616	
On c alone	.0609		.0854		.0855	
On total height (h)	.0543		.0663		.0772	
On ratio of c to h (r)[1]	.0345		.0391		.0316	
Variances (and standard deviations)						
Degrees of freedom (total)	225		367		298	
Total variance within plots	.1336	(.366)	.1315	(.363)	.1335	(.365)
About regr. on c and s	.0506	(.225)	.0572	(.239)	.0551	(.235)
About regr. on c	.0566	(.238)	.0598	(.244)	.0696	(.263)
About regr. on h	.0562	(.237)	.0680	(.261)	.0564	(.237)
About regr. on r[1]	.0774	(.278)	.0784	(.280)	.0982	(.313)
Squared correlation coefficients						
With c and s	.625		.567		.590	
With c	.579		.547		.481	
With h	.582		.484		.579	
With r[1]	.424		.405		.267	
With s	.028		.024		.116	

[1]Based on an approximation which overestimates the regression and correlation, underestimates variance.

cant and need confirmation by more extensive observations before any inference about this matter can be made.

Discussion

If the ratio live crown length/total height were an efficient indicator of diameter growth, the correlation of growth and stem length should be negative and of about the same order of magnitude as positive correlation to crown length. But these data indicate that the correlation is positive. Therefore insertion of height as a denominator in any compound to be used as an indicator of growth is contra-indicated. Its inclusion in that form can only reduce the correlation as compared to that with crown alone or with an optimum compound of the two characters. Our data suggest that a prediction of growth derived from the ratio may be less than two-thirds as precise as one based on a compound such as $3c + s = 2c + h$. Crown length alone may give 80 to 95 percent of the information available from crown and stem lengths together. Height, which may be easier to measure and is equivalent to weighting crown and stem equally, appears about as good as crown alone for comparisons within plots, but is not quite so good for comparisons between plots in the older plantings.

Considerable effort in the past has been spent to correlate crown dimensions with growth. Frequently the chosen criterion has been the ratio of live crown length to total height, but this choice seems to have been founded on arbitrary anticipation. Obviously, in evaluating two trees of the same height, comparisons of crown length or crown ratio are essentially the same thing. On the other hand, if two trees have the same crown size, the taller one has the

lower ratio; therefore, if the magnitude of the ratio were to serve, for example, as an index of vigor or of capacity to respond to thinning, it would indicate the taller tree as the poorer choice for a crop tree. Common sense dictates that this is a false conclusion and no forester would use it although it is the logical extension of what he says in other circumstances. We, therefore, suggest that silvicultural and mensurational investigations on crown size should explicitly deal with direct measures of that character itself unmasked by confusion with an arbitrary ratio.

Summary

In three young even-aged stands of loblolly pine, the 3-year diameter growth as associated with length of the live crown had a correlation coefficient about .75 and was slightly, but positively, related to stem length. In these circumstances, if crown length is to be used as an indicator of growing vigor, the crown size itself should be recorded. Moreover, use may be made of a compound, such as $3c + s = 2c + h$ (3 times the live crown length plus the stem length equals 2 times the live crown length plus total height), which weights crown size three times as heavily as stem length. The ratio crown/total height is actually not a satisfactory index. Its use assumes negative correlation between diameter growth and stem length; such correlation is not found in an even-aged stand. Consequently, it is a waste of labor to compute ratios which are poorer indices than the direct observations.

Many foresters may occasionally speak loosely of the ratio crown length/total height and seem to think in terms of that index. Yet unquestionably, while making tree-by-tree decisions on the ground, they are really concerned with the biologically significant variable of crown size itself. It is therefore suggested for mensurational investigations that recording the direct observations of crown size will save computing labor and encourage greater clarity of thought and exposition.

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The Vegetation of Wisconsin: An Ordination of Plant Communities

By John T. Curtis. Univ. Wisconsin Press, Madison, 1959. 657 + xi pp., 53 figs., 66 plates, 30 text tables, appendix, glossary, bibliography, species list, index.

Review by Stanley A. Cain
The University of Michigan, Ann Arbor

No American state has received a comprehensive analysis of its vegetation that approaches that set forth in *The Vegetation of Wisconsin.* Prof. Curtis has had two decades of field experience in Wisconsin and for more than a decade the Plant Ecology Laboratory has been the physical and intellectual center for community studies by colleagues and students directed and inspired by his leadership. Much of the success of this group can be attributed to the stimulation, perhaps excitement, of original concepts and methods for the study of plant and animal communities and their physical environment. Although there were antecedents in Gleason's individualistic association hypothesis, and the continuum concept of phenomena in nature was not new (*cf.* the catena in pedology), Curtis and the Wisconsin group made them their own by extensive exploration of the vegetation and biota that surrounded them. The general conclusions carry force not only by the reasonableness of the ideas; the weight of data are convincing. Perhaps for the first time since at the turn of the century when dynamic ecology burst on the consciousness of students under the leadership of Cowles and Clements, American ecology again has a school.

Just as the vitality of the concept of succession in earlier days had stimulated study of process in vegetation and, unfortunately, had obscured for some students the incompatibility of certain phenomena with prevailing orthodoxy; and as the practical usefulness of the association-type concept had forced all stands of vegetation into Procrustean beds of classificatory hierarchies; so had the quadrat method forced many compliant students into routine and wasteful field procedures that limited the scope of investigations to single stands or to the vegetation of local areas. Like the British who seem never to have been slaves to any system or methodology and whose work could culminate in Tansley's monumental *British Islands and Their Vegetation*, Curtis' school was never swamped by the complexities of supposed successional relationships, the multitude of associations which must result if one accepts literally the requirement of "typical composition and structure" of an association type, and the need for an almost unlimited number of quadrats if statistical significance is to be attributed to quantitative data obtained by their use. Relieved of such deterrents to the undertaking of a statewide study, the Wisconsin investigators set about a program which could be realized by a reasonable expenditure of time and money. Nevertheless a total of 1420 separate stands were investigated and they form the basis for the description of Wisconsin vegetation.

Instead of attempting to deal with the tremendous range in kinds of plant communities as types that are to be found in an area as large as Wisconsin and located so as to include within its boundaries three of the world formations of vegetation, for the purpose of analyzing and describing vegetational continua, Curtis subdivided the vegetation as a whole into 21 major and 13 lesser communities. On a basis of physiognomy the total terrestrial vegetation was divided into forests, savannas, and grasslands. Within these groups northern and southern subtypes were separated on a basis of floristic provinces. Finer subdivision was accomplished by a sort of compromise between the criteria of floristic composition commonly employed in Europe and the emphasis in North America on dominance. In general, dominance was important for the recognition of forest communities, prevalence in the non-forest communities, and physiography for minor communities (as in the case of beaches, dunes, and cliffs). When communities of a certain sort of vegetation are shown to form a vegetational continuum, convenience indicated an arbitrary subdivision into segments designated as wet, wet-mesic, mesic, dry-mesic, and dry, as in the northern forest, the southern forest, and the southern grassland. In addition there are four kinds of savanna, the northern grassland, and the boreal forest.

This is not the place to present in detail the

history of the continuum concept of vegetation, arguments and evidence for it, or details as to the ordination of plant communities; neither is it necessary to display here the new methodology of the Plant Ecology Laboratory, for the details are available in accessible literature and are summarized in *The Vegetation of Wisconsin*; yet something should be said for these matters still have to penetrate much of ecology and, in any case, it is this reviewer's opinion that the principal general contribution of Curtis' book will be along these lines, however interesting and useful the description of Wisconsin vegetation may be.

The idea that communities are real and may be discrete but that they are individualistic, and that association types are no more than approximations of convenience, had its roots in nineteenth century observations and its development in recent decades in many parts of the world. In the United States a clear statement of this can be attributed to Gleason (1926, 1939) and of the vegetation continuum to Curtis and McIntosh (1951). But as Curtis says of communities, in the present work, "Their lack of an inherent discreteness . . . does not prohibit their orderly arrangement into groups for purposes of study and discussion." Several biological phenomena combine to produce the continuum: the individuality of the ecological amplitudes and optima of the species; the importance of chance in the coincidence of propagules and the suitability of conditions for their establishment; and the phenomenon of dominance, for example. As Curtis says, ". . . the exact species to enter an area and the exact number of individuals of each species which succeeds are unique phenomena never to be repeated at any two places or any two times." All of the details presented in *The Vegetation of Wisconsin* are in full support of the existence of vegetation in continua.

As to the methodology, a whole new approach was developed (Cottam and Curtis, 1949) which consisted in the sampling of trees by the use of point samples rather than fixed-area plots and the determination of the space occupied per plant rather than the number of plants per unit of area. In the forest studies quadrats were used for ground vegetation (herbs, shrubs, seedlings) and in grassland and other non-forest vegetation presence was largely relied on. Certain environmental characteristics of the soil and microclimate were investigated in most stands so that later ordination of the stands was possible in relation to environmental gradients.

The first part of the book is devoted to background with chapters on Flora, Environment, Plant Communities and Their Distribution, and Vegetation Study Methods. This part is followed by 17 chapters in five parts which treat Southern Forests, Northern Forests, Grasslands, Savanna and Shrub Communities, and Lesser Vegetation. Part 7 concludes the book with chapters on Postglacial History, The Effect of Man on the Vegetation, and Interrelations of Communities. An Appendix of about 80 pages contains for each chapter of the vegetational description much summary data. For example, for the Southern Forest chapters there is a table giving adaptation numbers for the trees, maps of the original mesic, dry, and lowland forests and of the stands investigated, and for these forest types there are tables of average tree composition, structure, prevalent ground species, and a community summary. With these technical (but important) details segregated, and with abundant and excellent photographs, the text is reserved for pertinent and essentially uncluttered ecological discussions.

Finally, it should be noted that the importance of this book does not lie solely in its original materials, abundant as they are. Curtis has made effective use of all the collateral studies on Wisconsin vegetation, the flora (which, thanks to the work of the late Norman Fassett and his students, is comparatively well known), and related ecology, geology, pedology, climatology, etc. He is ever alert to the practical uses of scientific studies of vegetation, to the need for conservation of species and communities, and to the beauties and appeal of nature to the mind as to the eye.

Don't miss this book on the false assumption that it is only of local interest. It deals with universal phenomena and is of general interest and importance not only to those who think of themselves as ecologists and biogeographers but also to those who pride themselves as practical foresters and other kinds of managers of land and its renewable natural resources. Such "pure" science as this is not just an adjunct to management, it is the *summum bonum*.

An Explanation of Changing Lumber Consumption and Price

BY
I. IRVING HOLLAND

BADLY NEEDED GUIDES to the solution of some of the lumber industry's more pressing economic problems such as narrowing profit margins, continuing loss of markets, and rising costs can be provided only if we become better acquainted with ways to segregate and examine the fundamental aspects of these complex problems. Useful answers may very well depend on continued and careful examination of the fundamental economic supply-demand relationships involved in these problems, using all the theoretical, statistical, and institutional information presently and subsequently available.

In a paper dealing with this general problem Zivnuska (1955) employed an analytical approach utilizing economic theory, institutional knowledge and some of the available data on lumber production and price. Though not a complex analysis of supply and demand, this study yielded informative results and pointed the way to further study.

The approach followed in the present discussion also makes use of the economic concepts of demand and supply. It concerns itself primarily with interpreting past consumption and price in terms of changing demand for and supply of construction lumber, pointing out how these shifts or changes may have come about.[1]

In the course of the discussion reference is made to several concepts commonly used by economists. The first of these is *market demand* as used in the economic sense. It is viewed as a negative net relation between commodity price and quantity and represents, in schedule or curve form, the quantities which might be purchased by all buyers in a particular market at various alternative prices with all other factors affecting demand, such as consumers' income, preferences, and prices of other products, remaining unchanged. Changes in demand are viewed as shifts or changes in demand position in response to changes in one or more of the "other factors."

Three kinds of coefficients called demand elasticities are commonly used to describe the particular characteristics of a given commodity demand. A coefficient of price elasticity is a negative ratio of the percent-

[1]At times the legitimacy of discussing shifts in *theoretical* demand and supply functions when the actual mathematical form of these functions is unknown or imperfectly understood has been raised. It must be remembered that economic demand and supply concepts are frequently used merely as tools of analysis — admittedly imperfect ones — in attempts to erect at best very approximate models or descriptions of economic mechanisms which "explain" the generation of past data. If such tools are useful for this purpose, then it is appropriate to use them, or any other. Final judgment should be reserved for evaluating the performance of the *model* in prediction; models which "fail" to perform must be rebuilt using, perhaps, new information and perhaps different tools.

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age change in sales to a percentage change in price, all other factors being held constant; price elasticity varies from place to place on the demand curve. Demands for commodities with many good substitutes tend to be elastic with respect to price, meaning that over much of the demand curve given percentage changes in price will effect relatively larger percentage changes in sales. A coefficient of income elasticity is a positive ratio of the percentage change in sales to a given percentage change in income; the change in sales is brought about by a shift in the position of the demand curve, other factors being held constant.

A coefficient of *cross-elasticity* is a ratio of the percentage change in sales of one commodity to the percentage change in the price of a substitute or complement, other factors remaining unchanged. Again demand position is changed. Cross elasticities between substitutes are positive; between complements, negative.

The second concept is *market supply*. Market supplly is also used in an economic sense, i.e., a positive net relation between quantities of a commodity which all producers combined in an area would be willing to produce and offer for sale at alternative prices, other supply factors like factor costs remaining unchanged. Changes in market supply are viewed as shifts in position of this net price-quantity relation or curve when a change occurs in some factor such as price of labor or logs, manufacturing techniques, or number of firms in the industry. The firm's supply curve is a marginal cost curve. It shows, at least in theory, the cost of producing each additional unit of a product within a plant of given size using a given technique when output is varied, factor costs remaining unchanged. Market or industry supply curves represent the aggregation (horizontal summation) of all the firms' supply curves at some particular place and time.

Two kinds of coefficients describe the characteristics of supply. A coefficient of supply elasticity is a positive ratio of percentage change in production to some percentage change in price, all other factors remaining unchanged. As in demand, supply elasticities vary from point to point on supply curves. The more "flexible" is supply, or the larger the coefficient of supply elasticity, the more responsive output is to price change at that point. A coefficient of *cost elasticity* is a negative ratio of the opposite percentage change in output to a given percentage change in factor cost levels, all other factors held constant. With prices fixed, this represents a change in supply position. An increase in factor costs shifts a supply curve upward to the left, i.e., decreases supply. A decrease in factor costs shifts a supply curve to the right, or increases supply.

Over time, the position of industry supply may also be modified by a changing number of firms in the industry. For instance, as more firms enter into production supply curves are shifted to the right; i.e., supply is increased. This may happen despite the fact that there occurs, simultaneously, a tendency for the curve to be shifted upward to the left as factor costs rise under competition for productive resources. When firms leave the industry, supply curves tend to shift to the left and if many firms drop out, this occurs despite the fact that factor costs may be falling.

The discussion to follow will examine first the probable past changes in demand for construction lumber, pointing out possible reasons for the shifts. The discussion of demand is followed by an examination of past supply. Some working hypotheses regarding changing lumber supply characteristics are presented; changing lumber supply is related to rising manufacturing costs and to falling productivity in logging and milling. An attempt is made to show, in terms of changing demand and supply, how lumber prices have risen and total lumber consumption expanded only moderately between 1920 and 1955. Finally some future implications of continuing trends in the industry are briefly discussed, and some broad suggestions for reversal of

these trends presented.

Construction Lumber Demand

Between World War I and World War II, about 70 percent of all lumber consumed annually was used for construction purposes; in the period following World War II, 75 percent. Demand for construction lumber is a major determinant of total lumber demand and a principal factor influencing the volume of lumber consumed at any particular time. A complex of forces act to determine the size of lumber demand: viz., rate of population growth, rate of family and household formation, level of personal incomes and general economic activity, availability of mortgage credit, and general costs of land and construction. Other factors working overtime also influence demand; e.g., changing size of structures, architectural modifications reflecting changes in consumer preference, building codes, insurance rates, and the introduction of new and technologically superior materials as well as lower installation or maintenance costs connected with the use of these materials.

The average net effect of each of these interrelated influences is as yet imperfectly understood although some of the gross or combined effects of these and other factors can be observed in historical consumption data.[2] Since historical consumption and price are actually the resultants of past demand and supply interactions any inferences we care to make regarding demand alone during some particular period should rest upon some assumptions regarding supply during that period. In this discussion frequent reference is made to three periods in recent economic experience which have been relatively free of war-time and government price control disturbances; e.g., 1922-1929, 1930-1941, and 1947-1958. In order to discuss demand change in these periods, what can be said about supply?

In Figure 1 lumber price-lumber production coordinates representing annual supply-demand intersections were plotted for the three periods. A balanced straight line was hand fitted to each group of points. The year 1930 appears to be transitional between the 1920's and 1930's, and does not influence the trend lines as fitted. Lumber production data are based on Forest Service estimates for the years 1922-1941 and 1948, Bureau of the Census estimates for 1947 and 1949-1955, and the estimates of the National Lumber Manufacturers Association for 1956, 1957, and 1958. Lumber price data for the years 1926-1958 are from the Bureau of Labor Statistics Wholesale Lumber Price Index on a 1947-49 base; the index for the years 1922-1925 has been converted from the BLS index on a 1926 base to the 1947-49 base by the Forest Service. All price data are finally expressed in terms of constant 1947-49 dollars to remove the effects of changing general price levels through deflation by the BLS index of all commodity prices.

Zivnuska (1955) previously examined essentially the same kind of information in the same way. In this article he presented a chart quite similar to Figure 1. He concluded that the three lines can be considered as zones within which the intersections of supply and demand took place in response to short-term economic fluctuations in each period and the shifts between the lines represent the long-term trend in the level of these intersections. Although it was not possible to say exactly how either demand or supply has changed over this period, Zivnuska concluded that lumber demand has been subject to great cyclical shift and has at times reached low levels (the Great Depression). Over the long run, however, demand appears to have increased, reaching the highest levels in the post World War II period. These and other data also suggest that demand has

[2]Determination of average net demand and supply relationships, and estimates of demand and supply elasticities involve complex statistical analyses. Although these are referred to in a general way in this study, inferences concerning them are not necessarily based on the actual results of such statistical studies.

probably become more elastic over time.

Similarly, lumber supply has been subject to cyclical shift and over time has declined. In addition the data suggest that lumber output in response to changing lumber price tends to be inelastic at high levels of prosperity and more elastic when economic activity turns downward. Finally Zivnuska concluded that the lumber supply schedule is probably becoming more inelastic.

The trend lines of Figure 1 also show how, on the average, lumber production and price have been associated over the years in each group. We may not legitimately infer that these trend lines represent "supply curves" for they represent only intersections of demand curves at certain points on supply curves over time. However, according to Working (1927), if, over a given period, demand shifts have been large relative to shifts in supply, the intersections of demand and supply trace an "average supply response curve." If supply shifts have been large relative to changes in demand, the intersections trace a "demand response curve." In an analysis of this kind, as pointed out by Zivnuska, it is not possible to quantitatively measure the magnitude of net demand or supply shifts which appear to have occurred. The data suggest, how-

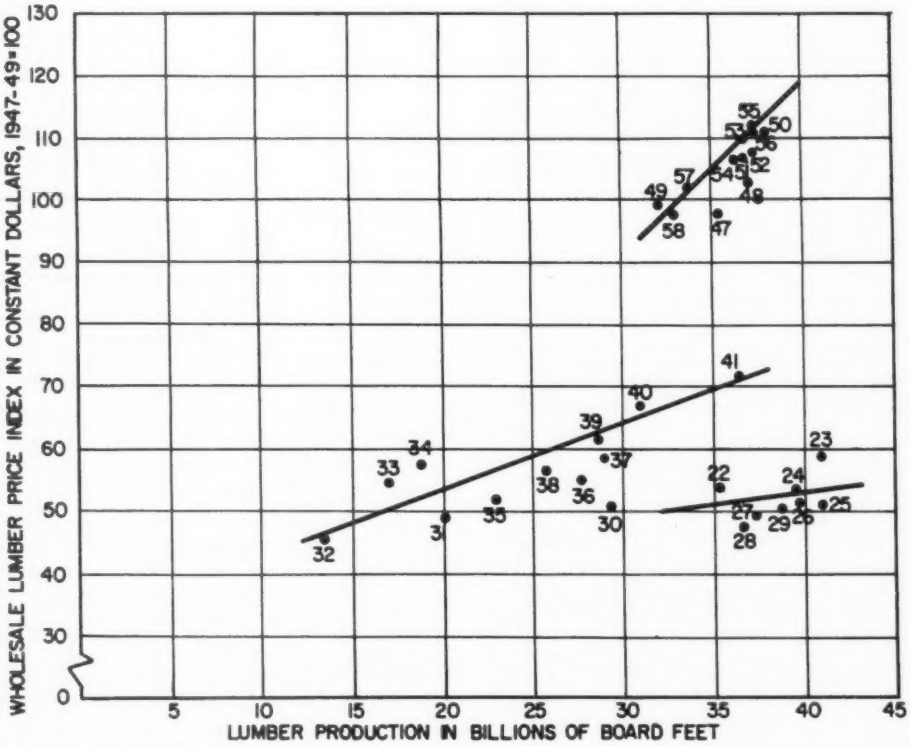

FIGURE 1. *Relationship between lumber production and the index of wholesale lumber price. (Lumber production 1922-1941 from Steer, 1948; for 1942-1955 from Census Series, Facts for Industry; for 1956-1958 from National Lumber Mfrs. Assn., Lumber Industry Facts, 1958. Price data from U. S. Bur. Labor Statistics Wholesale Lbr. Price Index in House Document 195, 85th Congress, 1st Session, 1957.)*

TABLE 1. Changes in lumber output and price, selected periods, 1922-1958.

Period	Output in MM bd. ft.	Index price in constant dollars	Change in output	Change in price	Percent change in output	Percent change in price	Ratio of percent change in output to Percent change in price
1922–1929	35	49.8	--	--	--	--	--
	36	50.5	1	0.7	2.86	1.41	2.03
	37	51.2	1	0.7	2.78	1.39	2.00
	38	51.9	1	0.7	2.70	1.37	1.97
	39	52.6	1	0.7	2.63	1.35	1.95
	40	53.3	1	0.7	2.56	1.33	1.92
	41	54.0	1	0.7	2.50	1.31	1.91
1930–1941	14	47.0	--	--	--	--	--
	17	50.0	3	3.0	21.42	6.38	3.36
	20	53.0	3	3.0	17.65	6.00	2.94
	23	56.0	3	3.0	15.00	5.66	2.65
	26	59.0	3	3.0	13.04	5.36	2.43
	29	62.0	3	3.0	11.54	5.08	2.27
	31	64.0	2	2.0	6.90	3.23	2.14
1947–1958	32	94.2	--	--	--	--	--
	33	97.1	1	2.9	3.13	3.08	1.02
	34	100.0	1	2.9	3.03	2.99	1.01
	35	102.9	1	2.9	2.94	2.90	1.01
	36	105.8	1	2.9	2.86	2.82	1.01
	37	108.7	1	2.9	2.78	2.74	1.01
	38	111.6	1	2.9	2.70	2.67	1.01

ever, that within all three periods, changes in demand have probably been relatively larger than changes in supply.

As plotted in Figure 1, then, the trend lines show, on the average, how production and price have been associated within each period. It is also possible through examination of these relationships to make some estimates of how changes in output and price were associated over each period as well as between the periods (Table 1). The figures in the last column are, of course, not true supply elasticities as defined earlier; they merely suggest how responsive production was to increases in lumber price over each period on the average. We may not logically compare the relatively high responses computed for the 1930-41 (Table 1) period with those or the 1922-29 or 1947-58 period because of the substantial differences in output range. During the depression period it is probable that demand intersected short-run supply curves over their lower or more elastic portions. However, as World War II approached, supply tended to become less responsive to increased price as indicated by the decreasing size of the ratios in the last column of Table 1. It is possible that in this part of the period demand curves intersected supply curves nearer their upper portions, supply had declined, or some combination of these events had occurred.

The output ranges for the periods 1922-1929 and 1947-1958 are similar, however, and it is possible to compare their production-price patterns. During the 1920's when output ranged from about 35 to 41 billion board feet increases in lumber price appear to have been associated with relatively large changes in production on the average; i.e., output response seems to have been greater than 1 or "elastic." During the post World War II period, however, when output varied between 33 and 38 billion board feet relative changes in price and output appear to have been associated only in about a 1 to 1 ratio. Furthermore, all

the ratios in the latter period are much smaller than the ratios in the earlier period; their closeness to unity would imply that output response to price changes was neither "elastic" nor "inelastic." Nevertheless, if we assume that production was affected within the upper portions of short-run supply curves in both periods, then the data suggest that supply was relatively more responsive to price change in the 1920's than in the postwar period. Decreased supply responsiveness between these periods could be attributed to declining supply over time, increasing inelasticity of supply, or some combination of these.

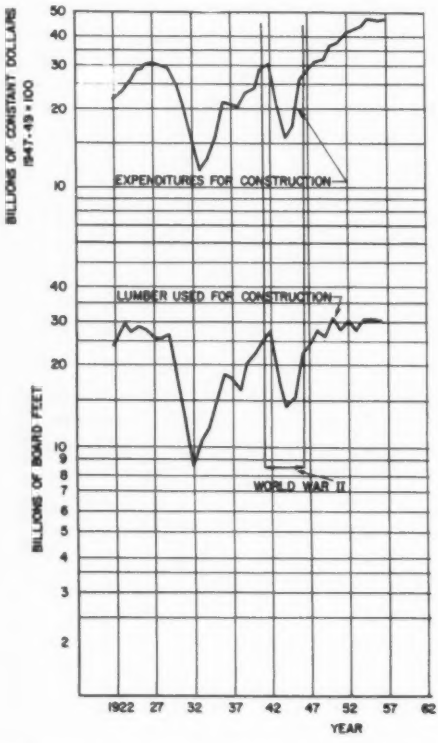

FIGURE 2. *Expenditures for construction and estimated consumption of lumber for construction, 1922-1956. (Expenditure data from U. S. Depts. Labor and Commerce, 1958a and b. Consumption data 1922-1928 from U. S. Forest Service, 1958b, and estimated proportion of lumber for construction from U. S. Forest Service, 1958a; source for 1929-1956 consumption data, and proportion used for construction, National Lbr. Mfrs. Assn., 1958.)*

For purposes of the demand discussion to follow we may tentatively assume that over the period 1922-1929 production was relatively more responsive to changes in demand and price compared to later periods. Between 1930 and 1941, other data (to be discussed later) suggest that lumber supply was probably not as elastic as during the 1920's and that the lumber industry was beginning to encounter relatively higher costs of production. During the post World War II period, indications are that expansion of lumber production has been more difficult despite high lumber demand and high prices.

Figure 2 compares expenditures for all construction including maintenance and repair expressed in constant 1947-49 dollars, and estimated consumption of lumber for construction purposes over the period 1922-1956. The U. S. Departments of Labor and Commerce have jointly published value estimates of new construction in actual dollars and in constant dollars (actual values deflated by appropriate cost of construction indexes) in Construction Volume and Costs 1915-1956 (1958a) and in Construction Review (1958b). To the value of new construction in constant dollars have been added the Department's estimates of the value of maintenance and repair which have been deflated by the Department of Commerce Composite Cost of Construction Index 1947-49 = 100. Total value figures are thus a measure of the annual physical volumes of construction.

Estimated annual volumes of lumber used for construction are based on Forest Service estimates of total apparent consumption which appear in Historical Forestry Statistics of the U. S. (1958b) and Forest Service estimates of the proportion of all lumber used for construction for the years 1922-28 as published in the Reappraisal of the Forest Situation (1946); for the years 1929-1956 the estimates are derived from

Forest Service estimates of total apparent consumption and the proportion of all lumber used for construction as computed by the National Lumber Manufacturers Association and published in Lumber Industry Facts for 1957 (1958). Volume of construction and consumption of lumber are plotted on semi-log paper, hence we may compare the slopes of the curves to detect differing rates of change over the period.

It will be noted in Figure 2 that the volume of construction rose to 1927, then fell rapidly to 1932. However, lumber consumption began to decline as early as 1925, and after 1929, fell more rapidly than volume of construction, indicating a loss in lumber market during this period. While in 1934 and 1935 lumber consumption appears to have increased faster than volume of construction, this advantage was apparently lost in the latter portion of the recovery period. In the postwar period, market loss is again apparent. Figure 3 shows these same data plotted in index form on arithmetic paper with 1922 equalling 100. In this case the *distance between the curves* suggests the magnitude of market loss. The situation in the postwar period is particularly striking.

Demand for lumber before World War II. Assuming that supply was relatively elastic during the 1920's and most of the 1930's, then changes in lumber consumption were brought about primarily through the action of demand factors. Major cyclical changes in lumber consumption over the period were related primarily to fluctuations in the demand for lumber and to changes in the volumes of residential and nonresidential construction. Loss of lumber markets in the period were very likely related to a secular decrease in consumption of lumber on a per structure or per unit of construction value basis. According to the Stanford study (Stanford Research Institute, 1954) the volume of lumber used per dollar of nonresidential construction decreased from 1.065 board feet in 1930 to 0.387 board feet in 1953. Between these same years the volume of lumber used per dwelling unit

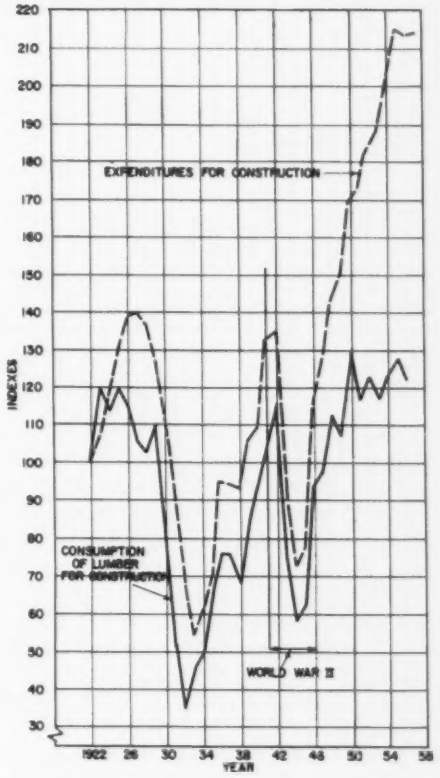

FIGURE 3. *Indices of construction expenditures and lumber used for construction, 1922-1956. 1922 = 100. (Data from same source as Figure 2.)*

(average all types) decreased 4900 board feet from 15,400 to 10,500 board feet; between 1920 and 1953 the loss was about 8,400 board feet. These losses can be "explained" in a variety of ways. However, it is proposed here that loss of lumber to substitute materials in both residential and nonresidential construction on a per unit basis during the period 1922 to 1931 was related primarily to actual decreases in demand for lumber because of decreased size of dwelling units, changes in the types of dwelling units constructed, and a shift away from lumber to other materials in nonresidential construction for technological rea-

sons. Between 1931 and 1941 it is believed that lumber use on a per unit basis was much more influenced by the rapid rise in relative lumber price which favored the expansion of other building material at lumber's expense.

It would be helpful to know if changes in the ratio of nonresidential to residential construction volume has significantly influenced consumption of lumber over time. Unfortunately data which could be effectively used to segregate these influences are not available. We do know that the volume of nonresidential construction (including maintenance and repair) as measured in constant dollars is consistently larger than the volume of residential construction (including additions and alterations as well as maintenance and repair). However, more lumber is used in residential construction than in nonresidential building. Finally, the ratio of nonresidential to residential construction has varied considerably over time. Based on the construction volume estimates (U. S. Dept. Labor and U. S. Dept. Commerce, 1958a,b), the average ratio of nonresidential to residential construction volume for the period 1922-1929 was 1.32; for 1930-1941, 2.35; for 1947-1957, 1.76. Thus, during the 1930's, nonresidential construction was relatively more important than during the 1920's and postwar period. However, the major shift away from lumber in nonresidential construction probably was accomplished before the 1930's and despite the greater relative importance of this kind of building during the 1930's it is likely that lumber losses occurring in this period were connected mainly with residential building. During the 1920's it is probable that substantial losses in lumber use occurred in both types of construction, while in the postwar period losses have been connected more with residential building.

Decreased size of dwelling units. Table 2 shows how the average size of dwelling unit has decreased. Table 3 indicates estimated lumber loss per average dwelling unit by house component over the period 1920-1953. Lumber loss per dwelling unit from all causes was 8400 board feet between 1920 and 1953. Averaging the data on floor space and cubic volume in Table 2, the Forest Service (1958a) computed for different years an average size-of-unit index and the approximate lumber content of a 1953 house of constant size as follows:

Year	Size of unit (index 1920 = 100)	Average lumber use per unit (bd. ft.)
1920	100.0	13,608
1930	86.0	12,894
1940	80.5	12,432
1950	72.0	11,697
1953	72.0	10,500

The displacement of lumber over this period amounted to 3100 board feet or 37 percent per dwelling unit at constant 1953 average size. This means that about 5300 board feet or 63 percent of total lumber loss per house was related to changing size of house. The size of unit index suggests that the largest decline in dwelling unit size per year occurred between 1920 and 1930.

Changes in type of dwelling units constructed. Demand for lumber in residential construction was also adversely affected during the period 1920-1940 because of the increased construction of 2-family and multi-family structures which, because of their size and location, greatly favored the use of building materials other than lumber, regardless of any other considerations. Ta-

TABLE 2. Changes in floor space, ceiling heights and cubic volume, average dwelling units, selected years, 1920-1953. 1920 = 100.

Year	Floor space	Ceiling height	Cubic volume
1920	100	100	100
1930	86	99	86
1940	82	96	79
1950	75	92	69
1953	76	90	68

Source: Stanford Research Institute (1954, p. 30).

ble 4 shows the trend in type of new dwelling units built between 1920 and 1955. The increased proportion of 2-family and multi-family structures during the 1920's reflects very largely the movement of labor from farm to cities in response to the heavy industrialization which took place in that decade. For reasons of permanence, strength, and safety, as required in building codes, these structures were most frequently made of concrete, steel, brick and other materials more suitable or technologically superior to lumber.

Changed price relationships. Some loss of lumber markets has resulted from changing lumber and competing materials price relationships. Figure 4 compares the Bureau of Labor Statistics Wholesale Lumber Price Index (1947-49 = 100) with a composite price index on the same base of materials which have competed with lumber over the period 1925-1955.[3] Figure 5 shows the ratio of the price index of lumber competing materials to the index of lumber price over this same period.

Both lumber and competing materials prices tended to fall between 1925 and 1932 (Fig. 4). According to the plotted price ratios in Figure 5, prices for lumber must have fallen more rapidly than for competing materials. If anything such a price relationship pattern would have favored the use of lumber over competing materials, other things being equal. Lumber price during this period was probably not a factor in depressing lumber consumption or

TABLE 4. Change in type of dwelling unit, selected years, 1920-1955.[1]

Year	Units		
	Single-family	Two-family	Multi-family
	Percent		
1920	82	10	8
1925	61	17	22
1930	69	9	22
1935	84	4	12
1940	85	5	10
1945	89	4	7
1950	85	3	12
1955	91	2	7

[1]Source: U. S. Housing and Home Finance Agency, (1956, p. 17).

[3]This index, constructed by the Division of Forest Economics Research, Forest Service, under the supervision of the Bureau of Labor Statistics, includes the following items: Douglas-fir plywood, insulating board, building sand and gravel, crushed stone, portland cement, concrete block, light colored facing brick, hollow building tile, plasterboard, structural steel, and reinforcing bars. After 1947 steel window sash, rubber and asphalt tile, and asbestos siding are included.

TABLE 3. Estimated lumber use per dwelling unit by house component, 1920-1953.[1]

Component	1920	1930	1940	1950	1953
			Board feet		
Foundations	1700	1350	1300	1100	900
Floors	4300	3700	3300	2550	1950
Ceilings	975	825	800	750	800
Roofs	2800	2250	2550	2600	2400
Exterior walls	2500	2350	2100	1750	1600
Interior walls	2950	2300	1700	1500	1500
Millwork	2600	1950	1400	1050	950
Accessories[2]	1075	675	750	400	400
Total	18,900	15,400	13,900	11,700	10,500

[1]Source: Stanford Research Institute (1954, p. 35).
[2]Accessories include porches and unattached garages.

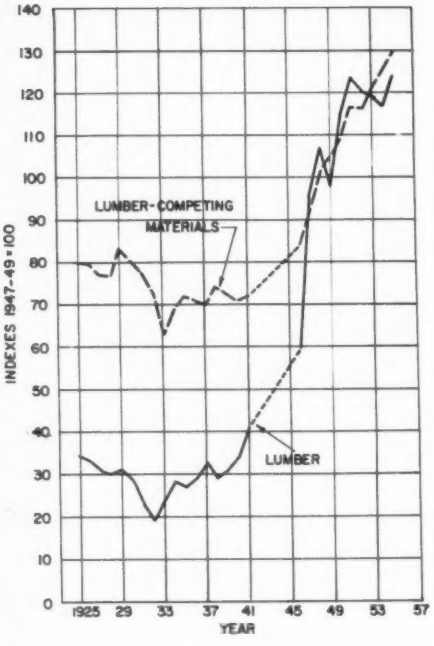

FIGURE 4. *Indices of lumber price and lumber competing materials, 1925-1955, 1947-49 = 100. (Data from U. S. Bur. Labor Statistics in House Doc. 195, 85th Congress, 1st Session, 1957.)*

encouraging expansion of markets for competing materials. Rather, as has been suggested above, decreasing lumber consumption per house resulted from declining lumber demand related to decreasing size of dwelling units, changing consumer preferences, and the need to use different nonlumber building materials.

Up to the time of the Depression at least, markets for nonresidential construction lumber were probably lost to competing materials largely because of greater strength and safety in use, lower maintenance costs and permanence of the latter, rather than because of high lumber price. Consumption again decreased through decline in demand. Although a very substantial volume of lumber is used in nonresidential construction, it plays a facilitating rather than a principal role. Most nonresidential construction use of lumber involves concrete forms, framing and trim material, scaffolding, bracing, shoring, decking and temporary buildings, and sheds.

The situation with respect to relative prices between 1931 and 1947 is very different. Very plainly in this period, price of lumber rose much more rapidly than did prices of competing materials (Fig. 5). Although some loss in lumber market took place during the 1930's and 1940's through substitution for reasons other than price, there may have been less room for substitution on this basis than before. With price spreads narrowed and old price relationships changed it is quite probable that market loss in more recent years can be attributed more to high relative lumber price than in the earlier period. The reasons for increasing lumber prices in this period will be discussed in more detail later.

Demand for construction lumber in the postwar period. Consumption of lumber for construction since World War II does not in general reflect the unprecedented high levels of demand for all kinds of building materials in this period. Even though

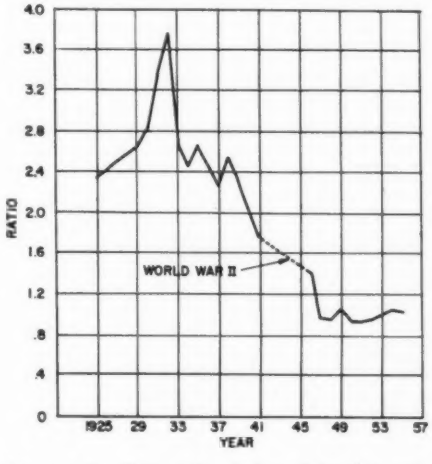

FIGURE 5. *Ratio price index of lumber-competing materials to price index of lumber, 1925-1955. (Data from same source as Figure 4.)*

lumber consumption has increased in response to greatly expanded building activity, this increase has been slower than for substitute materials; and lumber use has failed to keep up with increases in volume of construction (Fig. 2).

No precise explanation of the postwar lumber consumption pattern can be given, but it is possible to offer some interpretation of the facts that are available. Although there are no recent data available, it is very probable that the decline in lumber use per dwelling unit after 1953 (the last year for which data are available) has continued. Some further but slower decline in use of lumber per unit of nonresidential construction after this date is also possible. Thus, despite the large volume of building which has characterized this period, total consumption of construction lumber increased only moderately between 1947 and 1950, and none at all since that date.

In contrast to the period of the 1920's and early 1930's when supply is believed to have been relatively more elastic than after World War II and fluctuations in consumption were largely influenced by changes in demand, changes in consumption since 1946 have been affected by changes in both demand and supply. As noted earlier by Zivnuska (1955), lumber demand has probably become more elastic, due mainly to greater availability of substitutes while supply has tended to become more inelastic. Supposedly these modifications have occurred even as total demand has increased and as supply has declined. The overall pattern of high lumber price and a slowly increasing stabilized consumption are consistent with expanding total lumber demand and declining supply in the postwar period. Furthermore, the effects of these demand and supply changes on price and consumption have probably been heightened if, in the process, supply has become less elastic and demand more so.

Continued rise in lumber manufacturing and distribution costs stabilized to declining productivity in the industry have contributed to the postwar high price of lumber. The industry has experienced some difficulty in increasing output despite the high price of lumber. As will be noted later, industries producing substitute materials have not experienced this difficulty to the same extent. Demands for steel, aluminum, glass, brick and tile, asbestos siding, and other materials also expanded rapidly, after World War II, but production has tended to keep pace. Prices of these materials have also risen since World War II but not nearly as much as for lumber. Consumption of substitute materials has continued to increase.

Increased lumber price has also contributed to high installation costs. Of course, higher labor charges have also been involved. The combination of higher lumber price and the longer time required to put lumber components into place compared to the use of some other materials has acted further to hold down both per unit and total lumber consumption.

Lumber Supply

It has been suggested that decreased supply elasticity and declining supply because of rising costs have contributed to the lumber industry's problems through their influence on lumber price. The validity of this notion can better be evaluated after we have examined more closely the history of lumber supply.

In competitive industries like the lumber industry the response to increasing product price in the short run[4] is usually increased output on the part of member firms and the industry as a whole. Ordinarily in the short run, because some productive factor is fixed in total amount and variable fac-

[4]The short run is viewed as an indefinite period of calendar time during which output of the firm and the industry may be varied through changes in amounts of the productive factors used, but not through changes in scale or number of firms. The long run is a period of time long enough to effect production changes through variation in any or all factors of productions including the changing of plant size or industry organization.

tors are less efficiently employed as output is expanded beyond a certain point, greater output is forthcoming only at high marginal costs of production. At the same time, higher prices are required to call forth a larger output. Over the long run, output of the firm can be varied through changes in all factors including size of plant while industry output can be changed through modifications in size of the industry. The ease with which production can be varied when prices change depends upon the "elasticity of supply" and is supposedly reflected in the "shape" of supply curves.

The shape of a firm's supply curve and the response in production when price changes are dependent basically upon the manufacturing technique or process used, the size of the plant, and upon the degree of plant flexibility. The supply curves of firms where output can be varied over a wide range with relatively small change in cost are believed to be flat in shape; supply elasticities are relatively large. Those in which costs rise rapidly as rate of output is increased tend to be steep. In these firms it is difficult to increase output very much even if product price increases; supply elasticities tend to be relatively small.

Given some production technique or process, plant flexibility is basically a function of equipment divisibility and the adaptability of this equipment to varying kinds, amounts, and sizes of the raw material, and amounts of labor used in the manufacturing process. For example, a plant in which the manufacturing process can utilize a number of identical machines or groups of machines, and more than one kind, size or quality of raw material is said to be divisible as well as adaptable and can ordinarily expand or contract output within fairly wide limits without changing marginal costs per unit of output very much.

The milling of lumber always has been and still is very largely based upon a manufacturing technique that is not greatly amenable to modification; i.e. there are not many ways to saw boards from logs. Furthermore, the log sawing operation must be performed before further processing of the lumber can take place, and the speed of this operation sets the pace for further processing. Although various equipment and plant lay-out improvements have been made, particularly in the larger mills, no one has devised a radically different, cheaper, or otherwise more practicable way of making boards. The equipment used to make lumber in small or medium size mills, though it may be fairly adaptable, is almost always completely indivisible; i.e. the range of flexibility tends to be relatively narrow. In these mills there is usually only one headsaw and related equipment through which all the logs and boards must pass. The speed at which this equipment operates, especially the headsaw, very largely controls the operation of the mill. In such mills, not only may total physical capacity be reached quite quickly, but beyond a point considerably below full capacity, marginal costs may rise rapidly as output is increased. It is well known that low-grade lumber produced in small mills cutting small timber, even though investment in plant and equipment is low (or better *because* investment in plant and equipment is low) is still relatively costly to manufacture per thousand board feet because of high average variable costs. These mills use less capital equipment but much more labor per thousand board feet of lumber manufactured. Labor is expensive and becoming more so.

The equipment contained in larger mills may be more divisible in that there very often is more than one group of processing machines. This allows much more latitude for changing volume of output in any one working period with less change in unit costs of production. Furthermore, integration of several wood manufacturing processes which is possible within larger, better equipped plants or groups of plants has introduced much more output flexibility and contributed to higher productivity and lower costs through closer utilization of the basic raw material.

Decreasing supply elasticity. Over time, lumber output has varied both through changes in production from existing mills and from changes in the number of producers in the industry. When output increases in response to increases in demand and price a portion of the expansion is accounted for by the entrance into the industry of small, low-output but relatively high-cost mills. Greater pressure is put on the available factors of production, particularly logs, with the result that factor prices and manufacturing costs rise. Total production under these circumstances does not necessarily expand very much. In periods of declining lumber demand (as for example when the level of construction falls) production is decreased partly by elimination of small producers and through curtailed output in the larger mills. Costs tend to fall with some lag, but often production remains too high in relation to demand with a resulting downward pressure on prices because of higher inventories, and keen intra-industry competition for available markets.

The upward shift of firm or industry supply curves (decreasing supply) is associated with rising cost of manufacture. The rate of supply decrease is dependent upon the rapidity of labor, raw material, and other factor cost increases, and the action taken to counter these trends through increases in productivity.[5] Ordinarily, unless increases in logging and milling productivity keep pace with factor cost increases, manufacturing costs rise. If productivity increases substantially, costs may be lowered and supply increased. Although this has not happened very often in the lumber industry, it has and does happen in a number of other manufacturing industries particularly those which are growing rapidly. Rough as they are, available data suggest that lumber supply has declined steadily since the late 1920's.

As supply curves shift upward over time they also tend to become steeper. Expansion of output becomes more and more difficult—or less elastic even at higher prices. The lumber industry appears to be approaching this condition.

Decreasing supply elasticity has been related to declining productivity and rising manufacturing costs. As noted above the key to declining supply is to be found in changing lumber manufacturing costs and productivity over time. It is an old story in this industry. Except for a period in the 1920's, productivity has risen only slowly or has fallen, and unit costs of manufacture have tended to rise over time. According to Fabricant (1942) this is in sharp contrast to opposite trends in other manufacturing industries. Between the years 1899 and 1937 physical output of lumber mills declined 32 percent, number of wage earners declined 20 percent and wage earners required per unit of output increased 19 percent. To consider the period as a whole actually obscures the picture, however, and fails to show that during the period 1909 to 1929 productivity in the lumber industry actually increased somewhat. In more detail it is as follows: from 1899 to 1909, the number of wage earners required to produce a thousand board feet of lumber increased at an annual rate of 3.1 percent; between 1909 and 1919, and 1919 and 1929 requirements decreased at annual rates of 0.5 percent and 1.4 percent. Num-

[5]Productivity changes are meant to measure long-run progress. Productivity, or output per man-hour (the reciprocal of man-hours per unit), is the measure of the relationship between output in physical units and labor time. Labor time, however, is but one of the input factors. Productivity values do not measure the specific contribution of labor, capital, or any other one productive factor. Changes in the ratio between output and man-hours of work show only the gross effects of the operation of a large number of separate, interrelated influences including technological improvements, rate of operation, the relative contribution to total output of plants at different levels of efficiency, the availability of raw materials as well as the skill and effort of the labor force, the efficiency of management, and the state of labor relations.

ber of wage earners required increased again at an annual rate of 0.8 percent between 1929 and 1937. Thus, based on number of wage earners, productivity appears to have risen slightly only between 1909 and 1929. In terms of wage earner hours per unit of product the average annual rate of decline in the period 1909 to 1929 was 1.4 percent. This temporary increase in productivity was actually very low compared with most other manufacturing industries. Of a total of 38 industry groups, only six had lower annual rates of decline in man-hour requirements than did the lumber industry.

Considering the entire period further, the data also indicate that additions to capital assets of labor-saving equipment in the lumber industry did not occur at anywhere near the rates found in other industries. The adoption of improved plant layout, development of more efficient methods of manufacture and quality improvement practices did not proceed on nearly so wide a scale nor as rapidly as was the case in other industries. It is not surprising, then, that rising labor and stumpage costs coupled with a nation-wide trend to a shorter work week were reflected in increasing costs per unit of output, except perhaps in the period of the 1920's.

Actually between 1920 and 1929 the gradual shift to more costly logging of distant and inaccessible timber and the increasing cost of manufacturing lumber were effectively countered in the West by a steady decrease in man-hours required to produce a thousand board feet of lumber or logs. As shown in Table 5, this is a period in which large mills especially in the West became relatively more important.

Development in sawmilling which contributed to increased productivity in the West involved considerable capital investment. The introduction of faster machinery, the adoption of mechanical handling and conveying devices, and the elimination of much maintenance labor through electrification constituted important changes during the 1920's.

In the South the story was somewhat different. Adjustment in logging to lighter, sparser timber stands was made through adoption of more flexible logging equipment. In milling the trend was toward smaller though not necessarily more efficient mills. In the larger mills advancement took the form of greater electrification and better coordination of the sawmilling and handling processes.

Since 1935, the number of man-hours required to log and process timber in the South has increased (productivity has declined). According to the U. S. Bureau of Labor Statistics (1946) the number of man-hours required to saw a thousand board feet of lumber increased from 6.0 to 9.5 or 58 percent between 1935 and 1946. Planing time increased 42 percent and logging time requirements increased 34 percent.

TABLE 5. Lumber production by mill size-class, selected years 1919-1954.[1]

Mill size-class	Percent of total production in —						
	1919	1929	1938	1947	1952	1953	1954
Large	55.6	64.2	52.1	37.1	41.3	44.1	47.0
Medium	28.1	23.1	32.9	37.2	38.0	35.4	31.9
Small	16.3	12.7	15.0	25.7	20.7	20.5	21.1
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0

[1]Mill size classes are based on output in the particular year, and do not necessarily correspond to capacity: Large size mills 10 million board feet or over; medium size mills 1 million up to 10 million board feet; small size mills 1 thousand up to 1 million board feet.

Source: Bureau of the Census, U. S. Department of Commerce. In National Lbr. Mfrs. Assn. Lumber Industry Facts (1953 and 1957).

Data originating with the U. S. Bureau of Labor Statistics (1937) and the West Coast Lumbermen's Association (1949) indicate that productivity in logging and milling of Douglas-fir timber also declined between 1935 and 1949. Man-hour requirements per thousand board feet in logging increased from 4.9 to 5.1 or about 4 percent. However, it required 38 percent more time to manufacture a thousand board feet in 1949 than in 1935. For all operations, man-hour requirements increased 26 percent. Apparently the extension of access roads and widespread use of trucks, tractors, and other more flexible logging equipment has tended to overcome to a considerable extent the effects of increasing stand inaccessibility. As in the South, however, rising man-hour requirements in sawmilling and yard operations reflect decreasing average log quality, a trend to small mills, and to the greater degree of lumber finishing required to make the final product more acceptable in an increasingly competitive market for building materials. Reference to Table 5 indicates the decline in relative importance of large mills at least up to 1947 and the increased relative importance of small mills.

Since the early 1930's, but particularly after World War II, several factors have acted to increase logging and milling costs and to decrease supply in almost all major lumber producing areas: (1) declining availability of quality stumpage, (2) declining size and increasing taper of available sawlogs, and (3) increasing labor, log, and related costs. Industry productivity, which might have been raised through widespread adoption of technological improvements, integration of operations, and improvements in distribution and marketing has apparently not increased fast enough to effectively counter rapidly rising costs.

According to the most recent Forest Survey reports for Georgia and South Carolina (McCormack and Cruikshank 1949, 1954); Alabama, Arkansas, Mississippi, and Louisiana (Southern Forest Experiment Station 1953a and b, 1949, 1955) the number and average size of sawtimber trees is declining and larger proportions of timber stand volume are to be found in the smaller stand size-classes. In South Carolina there has been a marked increase in the number of hardwoods 1 to 5 inches d.b.h. between 1936 and 1947. Pole timber volume increased 15 percent while sawtimber volume declined by 10 percent.

In Alabama softwood sawtimber volume has declined 17 percent and hardwood sawtimber volume 5 percent since 1935-36. Based on the change in number of trees in each diameter class the average diameter of sawtimber trees declined from 12.7 to 12.2 inches.

Of the softwood sawtimber volume in Arkansas 17 percent was contained in trees 20 inches d.b.h. and larger in 1936. By 1951 less than 8 percent was in trees of this size. A similar trend in volume and tree size has taken place in the forests of Mississippi. However, in Louisiana, because of more intensive management on large private timber holdings, the average diameter of softwood sawtimber trees increased from 12.9 inches d.b.h. in 1934-35 to 14.9 inches in 1953-54. At the same time the average diameter of hardwood sawlog trees increased from 14.2 inches to 16.1 inches.

Almost all mill-scale studies indicate that milling efficiency falls and costs per thousand board feet rise sharply with decrease in log size, especially log diameter, particularly if log size falls below the optimum for which the mill equipment is designed. Not only do small diameter logs require more handling per unit of volume under these conditions, but the quality of lumber recovered from such logs often becomes lower with smaller diameters and greater taper. Manufacture of lower grade lumber frequently requires more processing than does lumber of higher quality. Logging costs in the South have also risen because improvement in technology and more efficient operation have not kept pace with increased labor charges, continued timber depletion, and the increased prevalence of

scattered light sawtimber stands with trees of smaller average volume and diameter.

Contributing heavily to increased manufacturing costs have been rising labor and raw material charges. Information on employment and earnings of the U. S. Bureau of Labor Statistics (1955, 1956, 1957a) shows that wages in sawmills and planing mills rose about 55 percent between 1947 and 1956; in logging camps, 38 percent. Labor charges are becoming more important in total lumber fabrication costs, not only because wages and salaries are rising, but also because an increasing amount of time has to be spent in manufacturing an acceptable product.

Figure 6 shows the trend in prices of Douglas-fir, southern pine and ponderosa pine stumpage, and also Douglas-fir logs over the period 1920 to 1956. Compared to the post World War II period, stumpage prices during the 1920's and 1930's were relatively low. Even though lumber and log prices increased, stumpage prices remained substantially unchanged. Rising manufacturing costs in this earlier period were more likely related to rising labor and other charges. After World War II, stumpage prices rose sharply; their influence on lumber supply through increased cost of logs in the post-war period has probably been quite significant. Table 6 shows that stumpage costs constitute a larger proportion of lumber price than ever before, and that most of the increase has come since the end of World War II. Actually, the data in Figure 5 probably underestimate the increase in stumpage costs because the present raw material is of a lower quality than the material logged during the 1920's and 1930's.

Although the discussion has centered

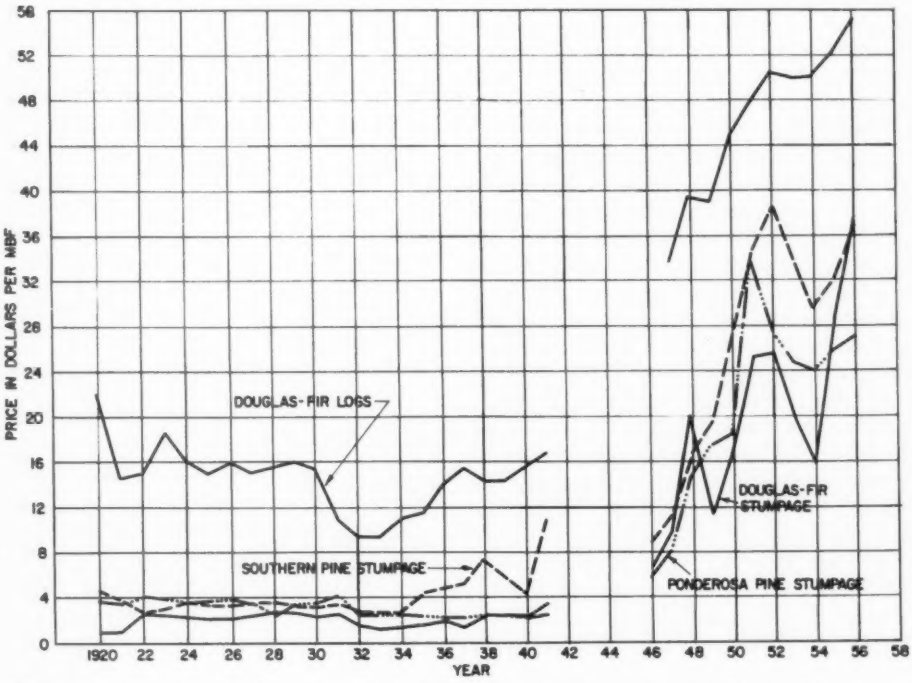

FIGURE 6. *Stumpage and log prices, 1920-1956. (Data from same source as Figure 4).*

TABLE 6. Douglas-fir stumpage price as a percentage of lumber price, 1910-1954.

Period	*Percent*	*Period*	*Percent*
1910-14	17	1935-39	10
1915-19	12	1940-44	11
1920-24	9	1945-49	18
1925-29	12	1950-54	28
1930-34	14		

Source: Eighty-fifth Congress, 1st Session. Price trends and relationships for forest products. House Document No. 195. 1957.

around manufacturing costs, it is of interest to note that rising transportation charges from mills to centers of consumption have certainly not helped lumber maintain its retail and wholesale competitive positions. For a long period preceding World War II, rail-freight charges showed little change, according to a study of forest products price trends made for the 85th Congress (1957) by the Forest Service. It cost an average of $20 per thousand board feet to ship Douglas-fir lumber from Seattle to New York in this period; rail shipments of southern pine from Mississippi to New York averaged about $12 per 1000 board feet. However, after the war freight charges for shipping Douglas-fir rose 75 percent by 1956, and the cost for southern pine increased 111 percent. Even intercoastal water shipment, which by 1930 accounted for some 85 percent of all lumber shipped from West to East, has fallen off drastically because of increasing freight charges. During the 1930's it cost only about $11 per 1000 board feet to ship lumber from the West to New York through the Panama Canal. Since 1951, however, water freight charges have exceeded freight charges on lumber shipped by rail. Increased transportation charges have acted to make lumber a relatively more expensive building material. Cost of transporting lumber has not been modified by "basing point" or other transportation arrangements used to considerable advantage, for example, by large producers of steel and cement.

Lumber demand and supply in retrospect. In retrospect the data suggest that during the 1920's productivity in the lumber industry rose, that stumpage costs remained relatively low, and that an increasing proportion of total lumber production came from the large, more efficient western mills. It may be reasonable to assume that under these conditions cost increases were effectively countered generally, and production response to change in price was relatively elastic compared to later periods. Since the early 1930's, however, rising costs have acted to decrease supply. In the process it appears that output has become less responsive to change in lumber price. In the period after World War II a less elastic lumber supply coupled with an expanded but probably a more elastic total demand have resulted in sharply rising price but only slowly increasing production and total consumption.

Using data on total lumber consumption and average lumber price and beginning with the 1920 situation, total demand increased sharply to 1925 in response to the increase in post World War I economic activity and the building boom. This was the case despite the decline in demand for lumber on a per unit basis because of decreased size of dwelling unit, the increased construction of multi-family urban units, and the shift away from lumber in nonresidential building. In this interval productivity in logging and milling probably increased, unit costs of production tended to remain stable and production rose substantially through increased output from existing mills and added production from new mills. The result was a 16 percent *increase* in lumber consumption accompanied by a *decrease* of 39 percent in lumber price.[6] Production increased 17 percent from 35 billion board feet to 41 billion board feet between these years.

After 1927, construction activity de-

[6]Consumption represents total production adjusted for imports, exports, and after 1935, changes in mill stocks as estimated by the U. S. Forest Service (1958b).

clined and total lumber demand decreased sharply (Fig. 2). As the economy plunged into deep depression many operations dropped out of the industry altogether and output of the remaining firms was cut back. There followed a period of depressed prices and relatively low production. By 1932 lumber production had fallen to about 13.5 billion board feet or 38 percent of production in 1920. Prices dropped more than 65 percent from 1920 levels.

By 1941 demand had recovered to a level somewhat lower than the high point reached in 1925, but a little higher than the level prevailing in 1920. During this interval, the industry again grew in size and production rose in response to increasing demand. Productivity in lumber manufacturing was probably higher in 1941 than it was in 1920 before the improvement in man-hours per unit was effected. If so, average costs of manufacture were quite likely also lower in 1941 than in 1920, but higher than in 1925. Furthermore, the industry was larger in 1941 than in 1920. At any rate, by 1941 consumption of lumber had increased to 36.2 billion board feet —23 billion board feet more than in 1932, but 4.5 billion less than in 1925. Price of lumber, though still lower than in 1920, was about 16 percent higher than in 1925.

Demand in 1950 and 1955, was much higher than in 1925, the earlier peak year. However, because costs of manufacturing had increased far beyond any prewar level, lumber supply had declined and consumption of lumber in 1950 and 1955 was very little different than in 1925. In contrast lumber price had increased over 230 percent by 1950 and 260 percent by 1955 from 1925 levels. Even under the tremendous stimulus of these very large price increases, lumber production in recent years has expanded only slowly. Furthermore, high lumber price, in addition to the other factors mentioned earlier, has acted to depress total lumber consumption and favor the demands for substitute materials. Apparently the trend to larger, more efficient mills, once more apparent after 1947, together with attempts to improve the lumber manufacturing process in some medium and small mills, has not been enough to counter declining supply and increased supply inelasticity for the industry as a whole.

Future lumber consumption and price. For the most part rising costs of labor and logs have been beyond the control of the industry and to a very large extent this situation will continue. Responsibility for raising productivity and thus modifying the trend in costs however, rests with each firm in the industry.

Major changes in lumber demand such as those effected by population and national economic growth are also quite beyond the influence of lumber manufacturers. However, important and beneficial secondary demand influences which could be effected by the manufacture and promotion of better, more useful lumber products at lowest possible cost, a primary consideration if the industry is to grow and share in the anticipated growth of the nation, are definitely within the control of individual firms and the industry as a whole.

Future total lumber demand has been given recent careful consideration both by the U. S. Forest Service (1958a) and the Stanford Research Institute (1954). In view of projected increases in population, gross national product, and construction activity total demand is expected to be much higher than at present. However, the magnitude of lumber demand at any particular time will be partly conditioned by the future utility and general availability of lumber products relative to supplies of competing products, and the future pattern of competitive building materials prices.

Labor charges both in manufacturing and construction will very likely continue to climb as the general standard of living rises. The costs of raw materials are also quite likely to increase for some time in most industries including the lumber industry. During the interval between complete liquidation of remaining virgin timber and increasing availability of second growth timber, stumpage prices will probably rise

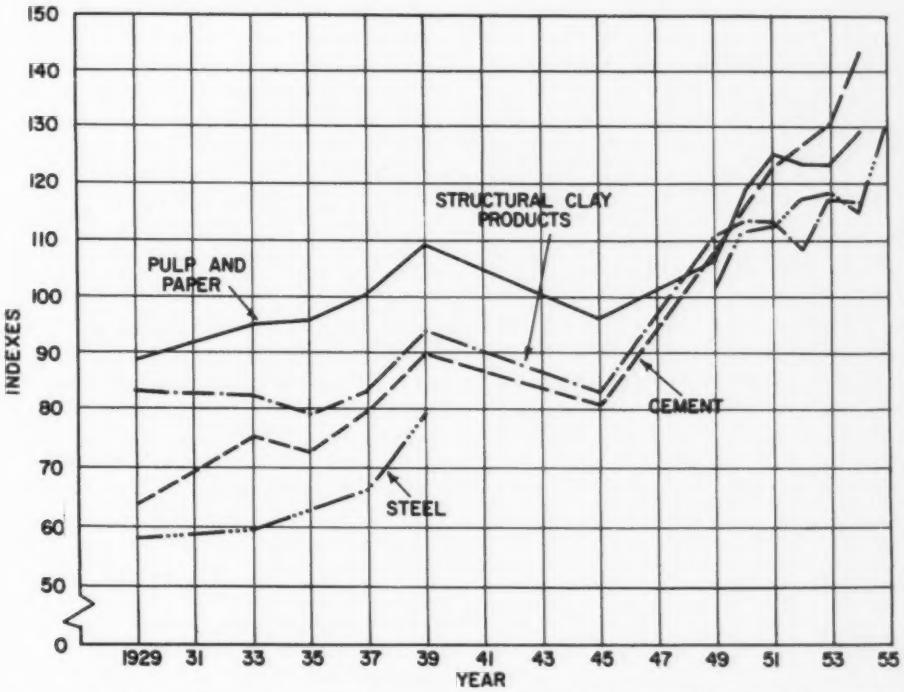

FIGURE 7. *Indices of output per man-hour in selected industries, 1929-1955. 1947-49 = 100. (U. S. Bur. Labor Statistics, 1957.)*

above present levels. To a considerable extent the ultimate level of stumpage price will be conditioned by trends in logging and manufacturing costs as well as future forest products price levels. It is quite likely also, that logs delivered to the mill will cost more in the future than they do at present because of increased labor charges, decreased accessibility, lower stand density, smaller tree size, and greater competition for available supplies. Timber quality will also continue to fall, furthering the increase in processing costs and making it more difficult to market quality products. Thus, lumber supply may continue to decline and supply inelasticity may become even more of a problem unless productivity can be raised very substantially.

Under these conditions lumber price would increase still further. At the same time total consumption of lumber would probably expand but very likely only slowly. Conceivably, if lumber prices should again rise more rapidly than prices of competing products, lumber consumption could be further affected adversely, and prospects for growth of the lumber industry would be dimmed.

Some of these same forces will also act in the industries competing with lumber and in the same direction. Considering past productivity and cost trends in these industries, however, it is not nearly so likely that costs will rise as rapidly or so far as in the lumber industry; demands for competing products will surely expand, but supplies will tend to remain more elastic. Figure 7 shows trends in output per man-hour for steel, cement, structural clay products and pulp and paper manufacture (U. S. Bureau

of Labor Statistics, 1957). In general, they are in sharp contrast to productivity trends in the lumber industry. In all these industries output expanded in response to higher demands after World War II, but even so prices have not risen nearly so far as they have for lumber. According to Bureau of Labor Statistics wholesale price data price of structural steel increased 104 percent between 1946 and 1955; price of brick and tile rose 74 percent; the composite price of building materials which supposedly compete with lumber in construction rose only 55 percent. In contrast, the price of lumber increased 110 percent over the same period. The fact that competing industries have been able to expand output and to increase consumption of their products (to lumber's detriment) at prices which have tended to rise much less than lumber price indicates what can be done when productivity increase is maintained and costs of production do not rise rapidly.

Conclusions and Recommendations

A continuation of past trends in lumber demand and supply relations will very likely lead to further loss of lumber markets through increasing demand elasticity and rising lumber price, and declining profits through increasing costs. A modification in these trends would seem imperative.

Much of the foregoing discussion has referred to the lumber industry and we have spoken in terms of aggregates. However, any changes which may be made in the interest of improving the future competitive position of lumber markets must take place very largely within individual mills. The analysis suggests that possibilities for changes on the demand side are not spectacular, will take time, and will require, concurrently, some basic changes on the supply side.

If lumber demand is to be reinforced, lumber manufacturers must produce a better, more usable set of products at lowest possible cost. Some of lumber's physical deficiencies as a competitive building material perhaps could be removed or reduced. For example, if lumber preservative and fire-retarding treatments could be more widely and economically applied, lumber might better compete in use with materials not subject to destruction by decay or fire. Perhaps more important is the need to adopt, as rapidly as possible, economically feasible methods of making lumber panels from lower quality material in order that lumber may better compete with the labor-saving sheet materials such as plywood, gypsum board, and fiberboards. Lumber quality and size should be more carefully controlled and standardized or it will not be able to compete favorably with materials such as aluminum, steel or plywood. The drive to develop new uses for lumber and to promote better public acceptance of lumber in construction should be continued and expanded.

Possibilities for substantial improvements on the supply side are somewhat brighter, although here also considerable effort and expense may be involved. Whereas lumber demand probably cannot be dramatically modified except perhaps over a long period of time, productivity in lumber manufacture (including logging) could be substantially raised with resulting lower costs of manufacture and increased supply elasticity, in a relatively shorter period.

Major efforts to control rising manufacturing costs in the lumber industry would seem to involve (1) maximization of wood products yield from costly raw materials, and (2) increased productivity in the manufacturing process to offset expected increases in labor charges. Techniques for extending the raw material through closer utilization of short lengths, slabs, chips, and edgings have been developed. It would be very helpful if their adoption were speeded up. Although some larger mills have been able to utilize their raw materials more closely through sale or integrated use of slabs, edgings, and chips for pulp, there is still much room for expansion of this procedure within the industry if economical ways of collecting the material from among the many small producers and distributing it

to pulp processors can be worked out.

Increased productivity, especially in milling, would go a long way toward countering expected increases in labor costs. This will not be easy in view of declining log size and average quality. Aside from adoption of better, faster, more accurate processing machinery, mill operators should give closer attention to plant layout and mechanical conveying and handling equipment. Reduction of time spent in moving lumber by hand would seem essential.

Ultimate responsibility for better utilization and higher manufacturing productivity rests with the firms which constitute the lumber industry. Organized lumber industry can also play a part, however through research into better methods of manufacture, new and better products, and the dissemination of this information to all interested members. Presently planned product promotional campaigns will surely be helpful, but a drive to promote widespread adoption of better equipment and more productive manufacturing procedures is equally important. Once developed, ways should be found for putting new ideas into practice as soon as possible. Production of quality products at lowest possible cost is the very essence of the problem at hand.

Considerable benefit by way of expanding lumber markets and lower costs will accrue to manufacturers and processors if improvements in supply and demand can be effected; this despite the fact that timber supply perhaps the ultimate limiting factor, tends to be inelastic and cannot be significantly increased except over a long time period. For some time to come the lumber industry will probably have to accept the fact that output expansion beyond a certain point may remain difficult despite substantial improvement in supply elasticity, because the holding of timber for anticipated higher stumpage price or for building up of growing stock under management will continue to limit available timber supply. To make the most of what will be available in the more immediate as well as the more distant future would seem to make good business sense, however.

Forest management will become an even more important objective than at present. Even if the industry solves its production and marketing problems, future expansion will be governed very largely by the supply of raw material. The problem of improving forest management especially on small forest holdings probably cannot be solved by industry effort alone, but will require the planned, coordinated efforts of the industry, individual forest land owners, and the interested public. The lumber and related industries should be expressly concerned with hastening the improvement of management on forest lands by whatever appropriate means that can be derived. A complete reliance on the eventual development of sufficient economic incentive to encourage better forest management on much of the nation's private forest lands will almost certainly work to the detriment of the lumber industry.

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